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British Museum (Natural History)

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"When one picks up a fish, one may be said, allegorically, to hold one of the knots in an endless web of netting, of which the countless other knots represent other facts, whether of marine chemistry, physics or geology, or other animals and plants. And just as one cannot make a fish-net until one has tied all the knots in their proper positions, so one cannot hope to comprehend this web until one can see its internodes in their true relationship."

BIGELOW (1930)

INTRODUCTION

IN both structure and function the teleost swimbladder is one of the most plastic of vertebrate organs. While it is primarily a hydrostatic organ, making a fish weightless in water, it may also be modified for respiratory, sensory and sound-producing activities (Jones and Marshall, 1953). Apart from the respiratory aspect, this statement is equally true of many deep-sea fishes. And the exception is understandable, for the use of the swimbladder as a lung is obviously limited to physostomatous teleosts, those with a pneumatic duct joining the sac to the foregut. Virtually all deep-sea fishes have a completely closed (physoclistous)[1] swimbladder.

Cuvier and Valenciennes (1848) appear to have been the first to discover a swimbladder in a deep-sea fish. Concerning the salmonoid genus *Argentina*, Valenciennes wrote as follows: 'La vessie natatoire de l'Argentine a un autre caractère anatomique et physiologique fort intéressant pour nos études; elle ne communique pas avec le canal digestif; je n'ai pu du moins trouver de conduit pneumatique dans les trois individus d'espèces différentes que j'ai disséques et dont les viscères étaient cependant parfaitement conservés.' (In the following volume (1850) they record the presence of a swimbladder in the hatchet fish, *Argyropelecus hemigymnus*.) Nearly forty years later, Günther (1887) made a similar observation in his 'Challenger' Report: 'In none of the abyssal forms examined by me have I found an open communication between the air bladder and the oesophagus, not even in those which are referred to the Physostomatous division.'

In defining the family Sternoptychidae, in which he included the deep-sea fishes, *Sternoptyx*, *Ichthyococcus*, *Maurolicus*, *Gonostoma* and *Chauliodus*, Günther (1864) stated that the swimbladder was simple when present. But under the family Scopelidae (containing fishes now placed in the order Iniomi) he remarked that the swimbladder was absent, a statement that is true with the notable exception of the lantern fishes (Myctophidae).

There are other observations on the structure of the swimbladder in Günther's 'Challenger' Report (1887) on deep-sea fishes. Further reference will be made to these later, but we may notice here that the rete mirabile of *Gonostoma denudatum* was described as a 'conical muscular body' attached to the posterior ventral part of the swimbladder. This confusion is hardly surprising, for the gas-secreting complex (retia mirabilia and gas-glands) of deep-sea fishes is highly developed. The large rete of *G. denudatum* contains thousands of closely associated arterial and venous capillaries

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[1] See page 50.

running forward in parallel to supply the gas-gland, and superficially these small blood-vessels look very like the fibres in a muscle.

However, a year before the publication of Günther's Report, Coggi (1886) had described certain structures in the swimbladders of *G. denudatum* and *Scopelus benoiti* (=*Hygophum benoiti*). He remarked that the 'red bodies' (retia mirabilia) of these two species were very like those of physoclistous teleosts and that the cells in the epithelial body (gas-gland) of *Gonostoma* were very large. In the other species Coggi figured three retia mirabilia, each supplying a corresponding lobe of the gas-gland. We shall see later that this is a constant feature of the myctophid swimbladder. But his finding of an opening into the 'pneumatic duct' is an error. Presumably he found the opening into the gas-resorbing part of the swimbladder, which in myctophids is an 'oval', and is placed at the front of the sac (see pp. 30–42).

Apart from this early account, the only other detailed work on the structure of the swimbladder of bathypelagic fishes has been that of Rauther (1922) on the lantern fish, *Diaphus rafinesquei* and Nusbaum-Hilarowicz (1920) on the hatchet fishes *Sternoptyx* and *Argyropelecus*, and a species of *Cyclothone*. Ray (1950) was the first to find and figure a fat-invested swimbladder, this being in the lantern fish, *Lampanyctus leucopsarus*. In his report on deep-scattering layers in the Monterey Bay area, Barham (1957) referred to work by Jollie (1954, Ph.D. Thesis) on the anatomy of this organ.

There are numerous records of the presence or absence of the swimbladder in both pelagic and benthic deep-sea fishes in Alcock's (1899) *Investigator* Report. Concerning benthic fishes only, Holt and Calderwood (1895) described the swimbladder of the deep-sea gadoid, *Mora* and those of certain macrourids. Presence or absence observations may also be found in Garman (1891) and in a few other papers which will be referred to in the descriptive part of this report. Lastly, Beebe and Vander Pyl (1944) gave the dimensions of the swimbladder in two lantern fishes, *Myctophum affine* and *Lampanyctus macropterus*, while Kanwisher and Ebeling (1957) measured the volume and gas-content of this organ in a number of bathypelagic fishes.

Considering only the observations made during the latter half of the nineteenth century, there is evidence that the swimbladder is found in numerous deep-sea fishes. But despite this early work, various authorities imposed a pattern on nature without further investigation. They decided that a swimbladder could not function in the deep-sea environment owing to the high hydrostatic pressures, and that it was therefore absent in deep-sea fishes. This organ is certainly absent in pelagic fishes whose living-space is centred below the 1000-m. level, but it is present in many fishes that swim above this depth and in numerous species living below, near the deep-sea floor.

The survey in this report has involved the examination of about ninety species of deep-sea fishes, certain aspects of which have already been published (Marshall, 1950, 1951, 1954, 1955; Jones and Marshall, 1953; Denton and Marshall, 1958). The first part is concerned with the description of the swimbladders of bathypelagic fishes. It will be found that this organ is commonly present in a number of major groups (e.g. the Gonostomatidae, Sternoptychidae, Myctophidae and Melamphaidae). In these and other fishes the gas-producing structures are highly developed.

In teleosts, the structural features of the swimbladder are not often of use in classification, but a gratifying feature of this survey has been the discovery that this organ has a distinctive design in the Stomiatoidea, deep-sea Salmonoidea, Myctophidae and Anoplogastridae. This aspect is considered in the second part of the report and leads to discussion of the evolution of bathypelagic fishes.

Then follow sections concerned with the larval organ, the fine structure of the swimbladder wall, and fat-invested swimbladders. In a number of species the swimbladder contains gas during the larval phase which is passed in the surface-waters, but the organ regresses and is invested with fat after metamorphosis to the adult form.

The remaining sections are devoted to functional-morphological and biological aspects. Now, development of the first aspect obviously depends on adequate knowledge of both form and function. Having undertaken a survey to the point where generalizations on morphology could safely be made, it was a pleasure to turn to the work of Dr P. F. Scholander and his colleagues on functional aspects of the swimbladder in deep-sea fishes. Full reference is made to this work at a later stage. In particular, Scholander's (1958) concept of counter-current exchange in the retia mirabilia and his review of this principle in biology has been very helpful.[1] I am also indebted to Dr Ragnar Fänge's (1953) fine work on structure and functions of the euphysoclist swimbladder. In the section on the swimbladder as a hydrostatic organ, findings on the structure of the retia mirabilia and gas-glands are considered in the light of this physiological work, a task that was made easier by my former collaboration with Dr F. R. Harden Jones (Jones and Marshall, 1953).

In the final biological section, the structural development (and absence) of the swimbladder in bathypelagic fishes is considered in relation to vertical distribution and vertical migrations. This has involved some consideration of the physical and biological environment and leads to the final part, which begins with a survey of the swimbladder in benthic deep-sea fishes. Considering only the fishes taken below a depth of 2000 m., at least half the number of species have capacious swimbladders. In the pelagic environment, as already mentioned, this organ is absent in fishes concentrated below the 1000-m. level. This surprising difference led me to consider, to use a concept more familiar to botanists, the 'life forms' of fishes from the upper and lower reaches of the bathypelagic environment. Again, I was helped by former collaboration, this time with Dr E. J. Denton (Denton and Marshall, 1958). The buoyancy balance-sheet of a fish with a capacious, gas-filled swimbladder is such that it can carry a firm skeleton and well-knit muscles. But these two tissue-systems and others are much reduced in pelagic fishes living below a depth of 1000 m., although this is not surprising in view of the poor food-supply around them. These fishes may well have lost the swimbladder simply because there is not sufficient potential energy in their environment to maintain the 'extra' tissues that can be carried by this hydrostatic organ. In pursuing this, and other ideas, I have tried to follow the thought behind the quotation that heads this report.

MATERIAL AND METHODS

Most of the fishes used in this report have been taken during the Discovery investigations. The positions at which they were caught are listed under the name of each species in the descriptive section (pp. 6–50) and unless otherwise indicated the station numbers refer to the Discovery collections.

In nearly all instances, the swimbladder was found by dissecting the fish under a binocular microscope. After noting the position of the organ, and where possible, tracing the blood supply, the swimbladder was removed and cut open so as to display the retial system and gas-glands. As these are well-developed in deep-sea fishes, their structure was readily appreciated. Where sufficient material was available more than one dissection was made.

In certain species (*Cyclothone braueri*, *C. livida*, *Argyropelecus olfersii*, *A. aculeatus*, *Polyipnus laternatus*, *Opisthoproctus soleatus*, *Vinciguerria attenuata*, *V. nimbaria*, *Myctophum punctatum* and *Diaphus dofleini*) the fine structure was studied by means of serial transverse sections. An account of this work appears in the sections dealing with the swimbladder wall (pp. 60–65), fat-invested swimbladders (p. 65–68) and the swimbladder as a hydrostatic organ (p. 68–81).

[1] To Scholander's list of organs in which this physiological principle is operative (the retia mirabilia of the teleost swimbladder, the gills of fishes, the placenta, the vertebrate kidney and the retial vascular structures of mammals) may be added the choroidal gland of the eyes of bony fishes (see Barnett, 1951).

In the descriptive section, measurements are given of the standard length of the fish dissected, the major and minor axes of the swimbladder (which approaches an ellipsoid in form) and the length of the retia mirabilia. Clearly, the dimensions of the sac in a preserved fish will be smaller than those occurring in the living state. However, in most specimens the swimbladder was well expanded. Where conditions were otherwise, this has been noted.

SURVEY OF STRUCTURE
CLASSIFICATION OF FISHES CONSIDERED IN THIS REPORT[1]
Order *ISOSPONDYLI*
Suborder STOMIATOIDEA (p. 7)

Family GONOSTOMATIDAE: *Vinciguerria attenuata* Cocco (p. 7); *V. nimbaria* Jordan & Williams (p. 9); *Pollichthys mauli* (Poll) (p. 9); *Bonapartia pedaliota*, Goode & Bean (p. 11); *Maurolicus muelleri* (Gmelin) (p. 11); *Gonostoma denudatum* Rafinesque (p. 13); *G. elongatum* Günther (p. 13); *G. bathyphilum* Vaillant (p. 13); *Photicthys argenteus* Hutton (p. 13) *Ichthyococcus ovatus* (Cocco) (p. 14); *Cyclothone signata* Garman (p. 15); *C. braueri* Jespersen & Tåning (p. 16); *C. livida* Brauer (p. 18); *C. microdon* (Günther) (p. 19); *C. acclinidens* Garman (p. 19).

Family STERNOPTYCHIDAE: *Argyropelecus aculeatus* Cuvier & Valenciennes (p. 19); *A. olfersii* Cuvier (p. 20); *A. sladeni* Regan (p. 21); *A. hemigymnus* Cocco (p. 21); *Sternoptyx diaphana* Hermann (p. 21); *Polyipnus laternatus* Garman (p. 22).

Family ASTRONESTHIDAE: *Astronesthes niger* Richardson (p. 23); *A. lucifer* Gilbert (p. 23); *A. gemmifer* Goode & Bean (p. 23); *A. similis* Parr (p. 25); *Borostomias antarcticus* (Lönnberg) (p. 26); *Diplolychnus mononema* Regan & Trewavas (p. 26).

Family STOMIATIDAE: *Stomias affinis* Günther (p. 26); *S. colubrinus* Garman (p. 27); *S. ferox* Reinhardt (p. 27).

Family MELANOSTOMIATIDAE: *Bathophilus metallicus* Welsh (p. 27); *B. pawneei* Parr (p. 27); *Eustomias obscurus* Vaillant (p. 27); *Echiostoma tanneri* (Gill) (p. 27).

Family CHAULIODONTIDAE: *Chauliodus sloanei* Schneider and *C. barbatus* Garman (p. 27).

Family IDIACANTHIDAE: *Idiacanthus fasciola* Peters (p. 27).

Family MALACOSTEIDAE: *Malacosteus niger* Ayres and *Photostomias guerni* Collett (p. 27).

Suborder SALMONOIDEA (p. 27)

Family OPISTHOPROCTIDAE: *Opisthoproctus soleatus* Vaillant (p. 27); *O. grimaldii* Zugmayer (p. 28); *Winteria telescopa* Brauer (p. 28); *Macropinna microstoma* Chapman* (p. 28).

Family MICROSTOMIDAE: *Xenophthalmichthys danae* Regan* (p. 28).

Family BATHYLAGIDAE: *Bathylagus benedicti* Goode & Bean* (p. 29); *B. glacialis* Lönnberg* (p. 29); *B. antarcticus* Günther (p. 29); *B. argyrogaster* Norman (p. 29).

Suborder CLUPEOIDEA (p. 30)

Family ALEPOCEPHALIDAE: *Bathytroctes rostratus* Günther* (p. 30); *Xenodermichthys copei* (Gill) (p. 30); *Searsia koefoedi* Parr (p. 30).

Order *INIOMI*
Suborder MYCTOPHOIDEA (p. 30)

Family MYCTOPHIDAE: *Myctophum punctatum* Rafinesque (p. 30); *Diaphus rafinesquei* (Cocco) (p. 30); *Electrona tenisoni* (Norman) (p. 32); *E. rissoi* (Cocco) (p. 32); *E. antarctica* (Günther) (p. 32);

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[1] Species or groups marked with an asterisk were not examined by the author.

Hygophum benoiti (Cocco) (p. 34); *Benthosema glaciale* (Reinhardt) (p. 34); *B. suborbitale* (Gilbert) (p. 35); *Diogenichthys atlanticus* (Tåning) (p. 36); *Myctophum humboldti* (Risso) (p. 36); *M. affine* (Lütken) (p. 36); *Diaphus dofleini* Zugmayer (p. 37); *D. garmani* Gilbert (p. 37); *D. luetkeni* (Brauer) (p. 37); *D. agassizii* Gilbert (p. 38); *Notolychnus valdiviae* (Brauer) (p. 38); *Lampadena chavesi* (Collett) (p. 38); *Lampanyctus güntheri* Goode & Bean (p. 38); *L. alatus* Goode & Bean (p. 38); *L. pusillus* (Johnson) (p. 40); *Gymnoscopelus nicholsi* (Gilbert) (p. 41); *G. townsendi* (Eigenmann & Eigenmann) (p. 41); *Gonichthys coccoi* (Cocco); *Ctenobranchus nigro-ocellatus* (Günther); *Diaphus coeruleus* Klunzinger and *Gymnoscopelus braueri* (Lönnberg) (p. 42).

Family NEOSCOPELIDAE: *Neoscopelus macrolepidotus* Johnson (p. 42); *Scopelengys tristis* Alcock (p. 43).

Family SCOPELOSAURIDAE (p. 43).

<div align="center">

Suborder ALEPISAUROIDEA (p. 43)

Order *MIRIPINNATI* (p. 43)

Order *CETUNCULI*

</div>

Family CETOMIMIDAE: *Ditropichthys storeri* (Goode & Bean) (p. 43); *Cetostoma regani* (Zugmayer) (p. 43).

Family RONDELETIIDAE: *Rondeletia bicolor* Goode & Bean* (p. 44).

<div align="center">

Order *GIGANTUROIDEA*: *Gigantura vorax* Regan (p. 44)

Order *LYOMERI*

</div>

Family EURYPHARYNGIDAE: *Eurypharynx pelecanoides* Vaillant (p. 44).

Family SACCOPHARYNGIDAE: *Saccopharynx ampullaceus* Harwood* (p. 44).

<div align="center">

Order *ALLOTRIOGNATHI* (p. 44)

</div>

Family STYLOPHORIDAE: *Stylophorus chordatus* Shaw (p. 44).

<div align="center">

Order *BERYCOMORPHI* (p. 45)

Suborder ANOPLOGASTROIDEA

</div>

Family STEPHANOBERYCIDAE: *Stephanoberyx monae* Gill (p. 45).

Family MELAMPHAIDAE: *Melamphaes megalops* Lütken (p. 46); *M. unicornis* Gilbert (p. 47); *M. mizolepis* (Günther) (p. 47); *M. cristiceps* Gilbert (p. 47).

Family ANOPLOGASTRIDAE: *Anoplogaster longidens* (Gill) (p. 47).

<div align="center">

Order *PERCOMORPHI* (p. 48)

</div>

Family CHIASMODONTIDAE: *Chiasmodon niger* Johnson (p. 48). *Pseudoscopelus scriptus* and *Dysalotus alcocki* (p. 49)

<div align="center">

Order *PEDICULATI* (p. 50)

Suborder CERATIOIDEA* (p. 50)

Order *ISOSPONDYLI*

Suborder STOMIATOIDEA   Family GONOSTOMATIDAE

Vinciguerria attenuata Cocco (Text-fig. 1)

</div>

St. 254, 35° 04′ 00″ S., 2° 59′ 30″ E., 21. vi. 27, TYF, 200(–o) m. B.M. Reg. no. 1930.1.12. 265–72. Standard lengths of two fishes examined 43·5 and 39·5 mm.

The swimbladder of this gonostomatid lies above the stomach and ends over the origin of the pelvic

fins (Text-fig. 1D). The sac is thin-walled and ellipsoidal in form, the measurements of the major and minor axes in the 43·5-mm. fish being 8·5 and 2·75 mm.
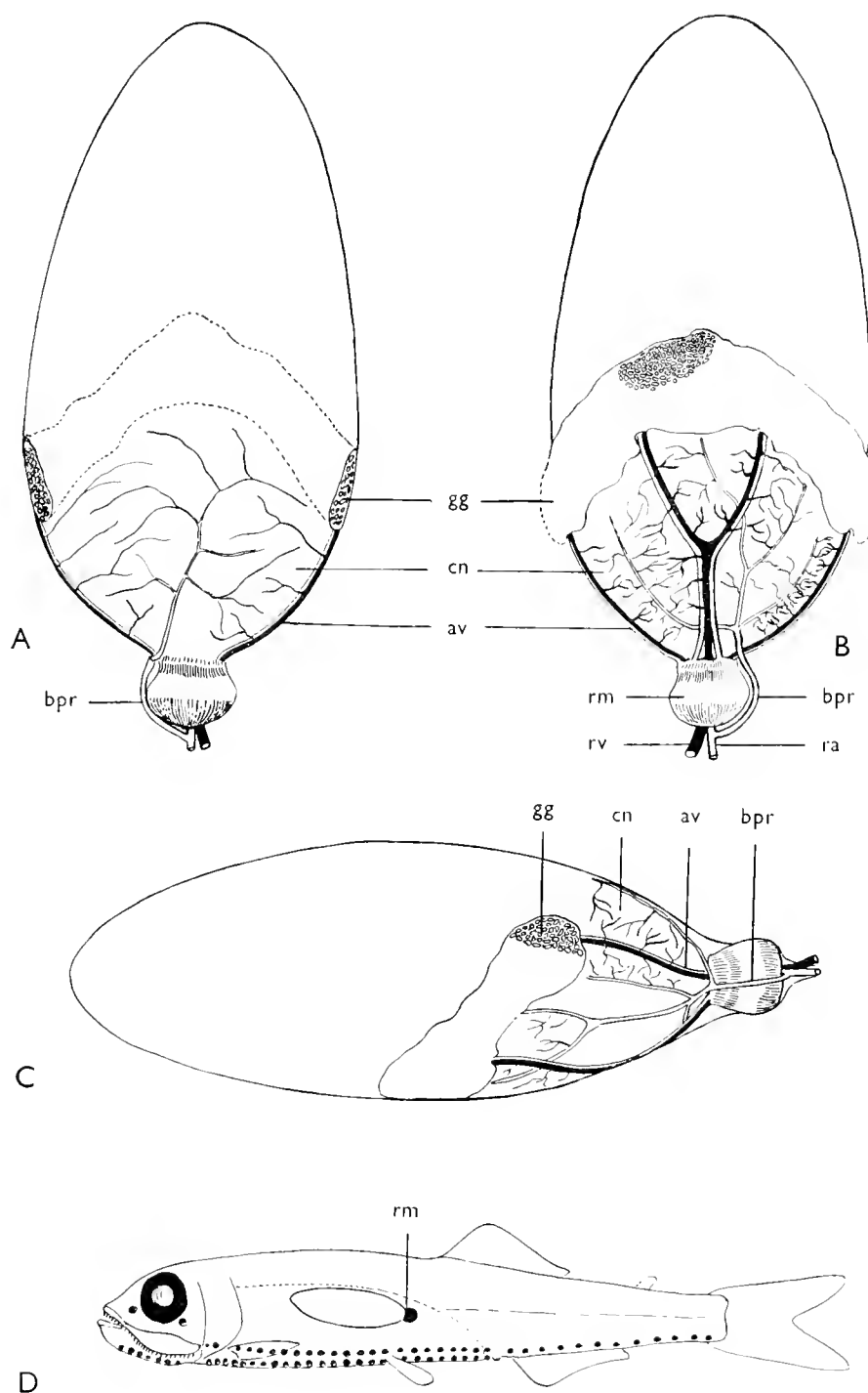
Text-fig. 1. Swimbladder of *Vinciguerria attenuata*, viewed: (A) dorsally; (B) ventrally; (C) laterally, and (D) in position in body-cavity of fish. Veins shown black, arteries white. *av*, artery-vein pair to gas-gland; *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (A, B and C, × 10; D, × 1·75.) Note on orientation of swimbladder, in this and subsequent figures. Where the swimbladder is drawn with the major axis vertical, the anterior end is uppermost. If this axis is horizontal, the anterior end is to the left.

In the larger fish, the rete mirabile, which is found at the rear end of the sac, is a massive cylindrical structure with a length and diameter of 0·8 mm. The gas-gland is a fairly broad transverse band of

tissue investing the floor and lateral walls of the sac (Text-fig. 1A–C). The forward, mid-ventral edge of the gland lies about half-way along the length of the swimbladder. The median part runs across the sac, while the lateral sections extend backwards and upwards to end just below the pigmented roof.

The rete mirabile is bipolar[1] in structure. It is formed from an artery and vein which break up into several thousand closely intercalated capillaries, these running parallel courses along the length of the organ. At the forward end they recombine into arteries and veins which supply the gas-gland. Two lateral artery-vein pairs enter the gland behind and just below its two upper edges, while there is a mid-ventral association of a vein with two flanking arteries. The vein runs forward to a point about half-way between the rete and gas-gland and then forks before entering the gland. The two arteries closely follow this venous path (see pp. 78–79 for stomiatoid blood circulation).

Behind the gas-gland there is an extensive capillary network running over the whole of the sac (and just below its inner epithelium). The arterial supply comes from a branch of the retial artery, which forks just before entering the rete. This branch runs forwards along the left side of the rete to a point just in front of it and then gives off a number of sub-branches. In ventral aspect, the vascular pattern may be appreciated by reference to Text-fig. 1B. It will be seen that the artery divides into three main sub-branches. Text-fig. 1C also shows that one main sub-branch travels to the roof of the sac and there subdivides into arterioles and capillaries.

. The capillary circulation is completed by the three veins to the gas-gland, which give off lateral venules. Those from the mid-ventral vessel and those from the lower sides of the two lateral vessels are associated with the arterioles of the three ventral sub-branches referred to in the last paragraph. The venules from the upper sides of the two lateral vessels divide to form capillaries that join those of the single dorsal arterial sub-branch.

This capillary circulation forms the resorptive part of the swimbladder, the region where gases diffuse into the blood when deflation of the sac becomes necessary.

The swimbladder of the smaller (39·5 mm.) fish has a very different appearance although its structure is basically the same. But the comparison of these two swimbladders, coming from fishes taken in the same haul, will best be left to a later section (p. 64–65).

Vinciguerria nimbaria Jordan & Williams

St. 1768, 33° 49·8′ S., 12° 50·8′ E., 19. v. 36, N 100 B, 290–150(–0) m. Standard length of fish 34 mm.

The structure of the swimbladder of this species is much like that of *V. attenuata*. The major and minor axes of the ellipsoidal sac measured 5·5 and 2·0 mm.

Pollichthys mauli (Poll) (Text-fig. 2A–C)

St. 273, 9° 38′ 00″ S., 12° 42′ 30″ E., 31. vii. 27, N 100 B, 118(–0) m. B.M. Reg. no. 1930.1.12. 254-9. Standard length 43 mm.

This species has a capacious, thin-walled swimbladder occupying much of the upper part of the body cavity. The sac is ellipsoidal, the measurements of the major and minor axes in the above fish being 5·0 and 2·2 mm. The posterior part of the organ fits snugly into a recess in the fore part of the enlarged, rear section of the kidneys, while the anterior end lies above the stomach.

At the posterior extremity of the sac is a single, bulbous rete mirabile (length 1·2 mm.), which supplies a horseshoe shaped gas-gland investing much of the floor and lateral walls of the swimbladder. The gland fits round the rete and encircles an oval-shaped capillary area, which is set in the middle part of the floor.

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[1] See also page 69.

2
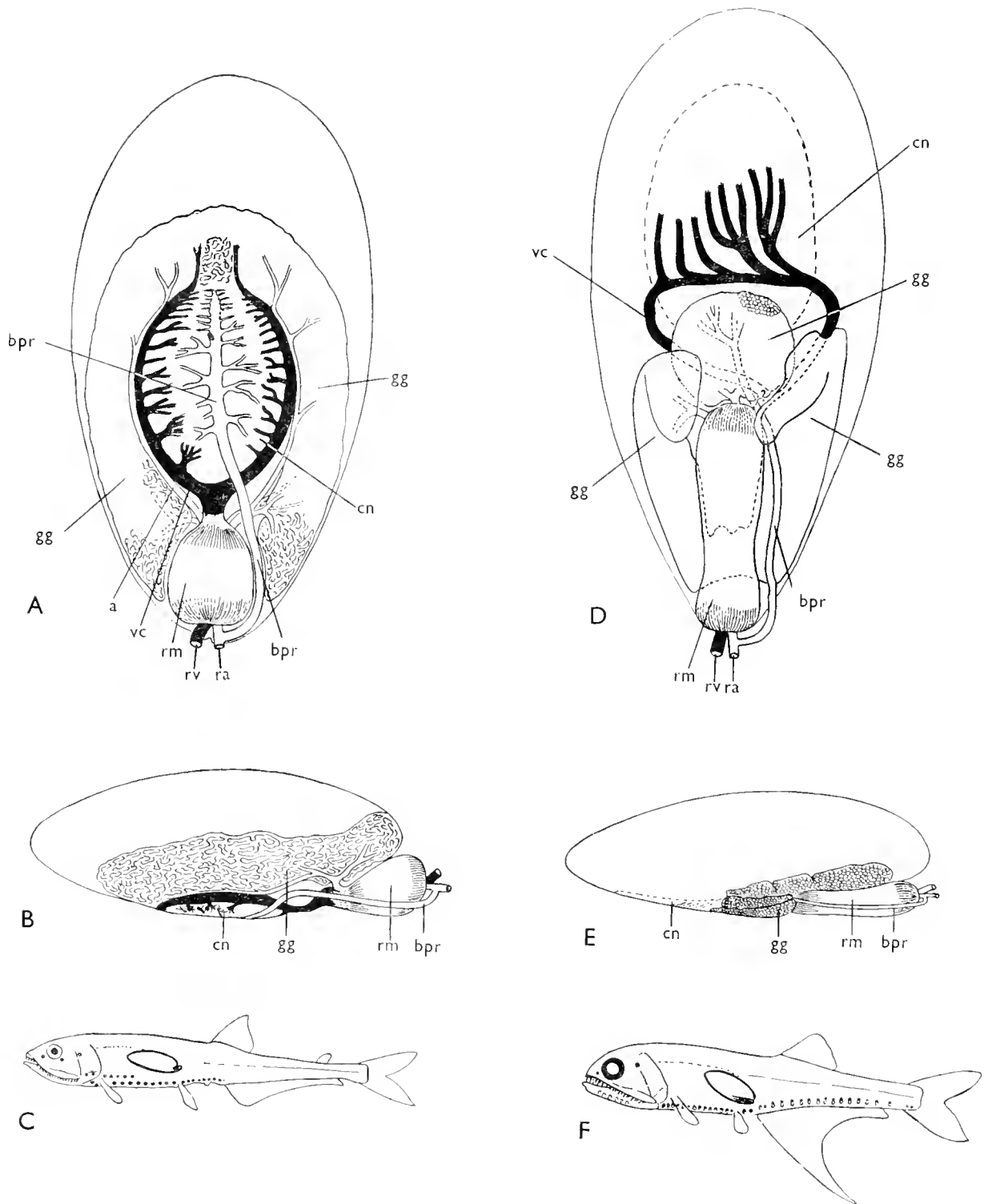
Text-fig. 2. Swimbladders of *Pollichthys mauli*, viewed (A) ventrally, (B) laterally, and (C) in position in body-cavity of fish, and *Bonapartia pedaliota*, viewed (D) ventrally, (E) laterally, and (F) in position in body-cavity of fish. Veins shown black, arteries white. *a*, artery to gas-gland; *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile, *vc*, vein to capillary network. (A, × 20; B, × 12·5; C, × 1·5; D, × 10; E, × 6; F, × 0·9.)

The rete, like that of *Vinciguerria*, is bipolar. At the forward end is a large median vein which soon forks to send branches round the inner edges of the gas-gland. Each of these two branches is accompanied by an arterial vessel, an association supplying the anterior parts of the gland. The posterior parts on either side of the rete also receive two artery-vein pairs (see Text-fig. 2).

The capillary network, through which gas may leave the swimbladder, is fed with arterial blood through a vessel coming from the retial artery. This by-passes the rete and runs forward along the mid-ventral line to give off arterioles that break up into capillaries. The venous part of the circulation comes from the large median vein of the rete.

Bonapartia pedaliota Goode & Bean (Text-fig. 2 D–F)

St. 1582, 05° 39·1′ S., 46° 22·3′ E., 29. iv. 35, N 450 II, 1900–1850(–0) m. Standard length 67·0 mm.

The swimbladder of *Bonapartia* is a thin-walled, capacious ellipsoidal sac lying immediately in front of the enlarged posterior part of the kidneys. When fully expanded it is likely to occupy more of the body cavity than that shown in Text-fig. 2 F. The major and minor axes of the sac measured about 10·0 and 5·0 mm.

A large club-shaped rete mirabile (length 3·6 mm.) runs under the posterior part of the swimbladder floor. Again it is bipolar in structure, supplying the gas-gland through vessels that are formed by the capillaries when they reach the anterior end of the organ. The gland, which is a single structure, fits closely round the rete. Its form may best be appreciated by reference to Text-fig. 2 D.

Immediately in front of the gland, and on the floor of the sac, is an oval-shaped capillary region. As in *Pollichthys* and *Vinciguerria*, the arterial part of the circulation is provided by a branch of the retial vessel. The venous part could not be traced in its entirety but seems to arise from two vessels running forward through the gland. (These veins may also provide part of the glandular supply.)

Maurolicus muelleri (Gmelin) (Text-fig. 3)

St. 2072, 46° 31·6′ N., 07° 42·9′ W., 22. v. 37, TYFH, 170(–0) m. Standard length 22 mm.

As in other gonostomatids, the swimbladder of *Maurolicus* lies forward of the posterior part of the kidneys. The major and minor axes of the ellipsoidal sac spanned 4·5 and 2·0 mm. The walls were quite thin, having a thickness of between 10 and 20 μ.

A single rete mirabile (length 0·75 mm.) is found at the posterior end of the sac and is formed by an artery from the dorsal aorta and a vein from the cardinal vessel (between the kidneys).

The gas-gland is four-lobed. Two smaller, rounded lobes lie above and to the side of the front part of the rete. The two larger lobes are oval in shape and extend over the floor and side walls of the middle section of the swimbladder. The long axes of these two lobes are parallel to that of the sac and measure 1·4 and 1·5 mm., the left being the larger. Each lobe receives a closely associated artery-vein pair emerging from the front of the rete, which is thus bipolar in structure.

There is a fine-meshed network of capillaries (the resorbent surface) lying just below the inner epithelium of the sac and between the lobes of the gas-gland. The median ventral area between the two larger lobes extends forward beyond their anterior ends, while the two lateral areas between the small and larger lobes extend upwards over the side walls of the sac. The arterial supply to the capillary network comes from a branch of the retial artery, which runs forward under and beyond the rete to a point close in front of its distal end, where it divides into three sub-branches. Two of these run outwards, each between the corresponding small and large lobe of the gas-gland. The third sub-branch proceeds forward along the mid-ventral line between the two large glandular lobes. These three vessels give off lateral arterioles, which break up into capillaries. The four veins to the gas-gland lobes complete the capillary circulation, each vein sending off branches that partly encircle the

lobe supplied. The forward and lateral edges of the two smaller lobes have a vein running round them, while the whole of the inner edges and about half of the outer edges of the larger lobes are similarly supplied with a venous system. The periglandular veins give off venules that divide again and again to form a dense capillary system, which is eventually linked with that formed by the branch of the retial artery. (The arteries to the lobes play no part in this capillary formation and do not branch until they have entered the gland.) The pattern of arterioles and venules can best be appreciated by reference to Text-fig. 3 A.

This extensive capillary complex forms the resorptive region whereby gases diffuse out of the swimbladder and into the blood stream.
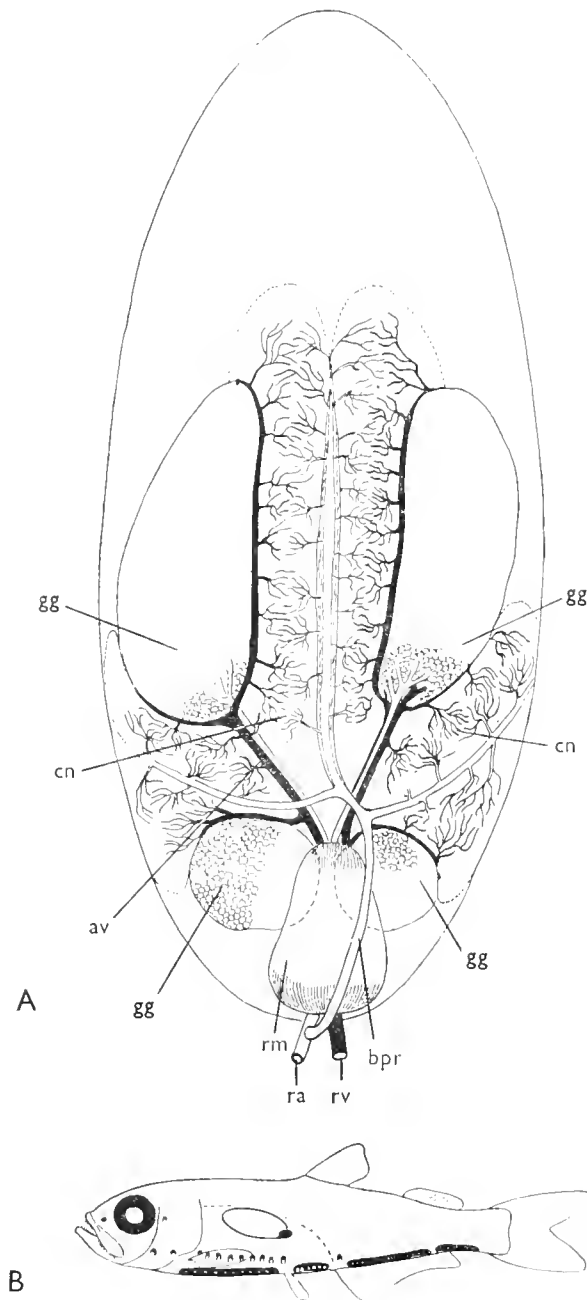
Text-fig. 3. Swimbladder of *Maurolicus muelleri*: (A) viewed ventrally, and (B) shown in position in the fish. Veins shown black, arteries white. Note the two small and two large lobes of the gas-gland. *av*, artery-vein pair to gas-gland; *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile, (Swimbladder, × 30; fish, × 2.)

Before continuing this survey, certain generalizations may be introduced at this stage. By doing so the descriptions can be more readily followed and needless repetition avoided.

We have seen that the swimbladders of the foregoing species of gonostomatid fishes have certain common features. These are: (1) a single, bipolar rete mirabile, which is formed at the posterior end of the sac, and (2) a resorbent capillary system that obtains its arterial supply through a by-pass branch of the retial artery. These characters are also shared by other stomiatoid fishes with a well-formed swimbladder in the adult phase. Furthermore, the first feature, at least, can be traced in adults with a regressed swimbladder. In the following descriptions, unless otherwise stated, the lengths of the major and minor axes of the sac are given in parenthesis after the standard length of the fish.

Gonostoma denudatum Rafinesque (Text-fig. 4A)

B.M. Reg. no. 85.6.22. 73–6. Messina. Standard length 81 mm. (16·0 × 2·0 mm.)

The swimbladder is elongated and fits close beneath the kidneys, extending down some two-thirds of the length of the body cavity. It originates above the bases of the pectoral fins and ends over the pelvics. Reference to Text-fig. 4A will show the close reciprocal relations between the shapes of the swimbladder and kidneys.

The bipolar rete mirabile, which is club-shaped and about 2·5 mm. in length, runs straight into the posterior end of the swimbladder floor. It is formed from two vessels running down through the kidneys from the dorsal aorta and the cardinal vein. The gas-gland invests most of the swimbladder floor and also extends over the lateral walls of the wider, posterior part of the sac.

Just before its point of entry, the retial artery gives off the by-pass branch to the capillary system. Although not traced, this system must be formed immediately in front of the more extensive, posterior part of the gas-gland.

Gonostoma elongatum Günther (Text-fig. 4B, C)

St. 285, 2° 43′ 30″ S., 00° 56′ 30″ W., 16. viii. 27, 125–175(–0) m. B.M. Reg. no. 1930.1.12. 74–7. Standard length 149 mm.

At first sight the swimbladder appears to be completely absent in this species. In place of the long gas-filled sac found in *G. denudatum* is a long rod-like mass formed of golden-yellow fat globules suspended in a reticulum of connective tissue cells. At the posterior end of this rod the fatty tissue extends over a small cream-coloured body that receives an artery and vein running down through the posterior enlarged part of the kidneys (see Text-fig. 4C). These vessels are clearly homologous with those forming the rete mirabile in *G. denudatum*. In fact, the creamy-coloured tissues to which they lead are the remnants of the gas-gland and rete mirabile.

Gonostoma bathyphilum Vaillant

No trace of a swimbladder could be found in this species, not even in a fairly young fish (standard length 77·5 mm.) from St. 3094, 44° 20′ N., 16° 49′ W., 21. v. 54, TYFH, 1500(–0) m.

Photichthys argenteus Hutton (Text-fig. 5)

St. 101, 33° 50′ to 34° 13′ S., 16° 04′ to 15° 49′ E., 15. x. 26, N 450 H, 350–400(–0) m. Standard length 141 mm. (4·5 × 2·0 mm.).

The swimbladder of *Photichthys* is unusual in form. The sac is a long tube originating over the stomach and extending down about three-quarters of the length of the body-cavity.

At the posterior end is an ellipsoidal bipolar rete mirabile, which is rather more than 3 mm in length and about 1·5 mm. in middle depth. The capillaries of the rete are formed by two vessels coming from the dorsal aorta and cardinal vein (between the kidneys).

The gas-gland invests the walls of the sac over a length of about 10 mm. in front of the rete. As the swimbladder was quite relaxed the walls appear to be rather thick.

Günther (1887) dissected a *Photichthys* taken by the 'Challenger' Expedition and described the swimbladder as a 'long simple sac with thick walls'. As already mentioned in the introduction, the 'conical muscular mass' at the posterior end is clearly the rete mirabile.
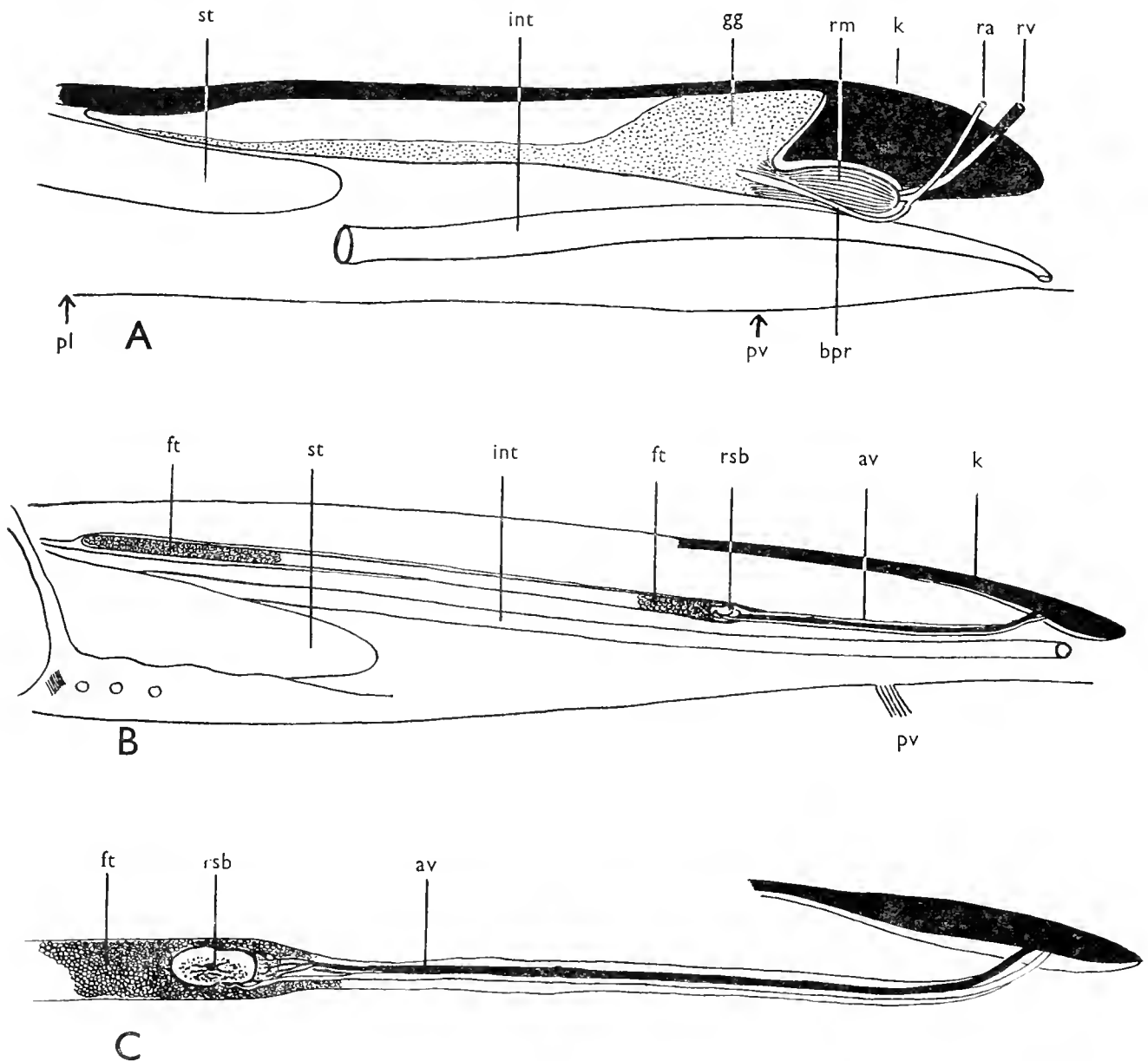
Text-fig. 4. Swimbladder of (A) *Gonostoma denudatum* (lateral view), and (B, C) *G. elongatum* (lateral views). In (C) the regressed swimbladder is shown enlarged with part of its investment of fatty tissue. *av*, artery-vein pair to regressed swimbladder; *bpr*, by-pass branch of retial artery; *ft*, fatty tissue; *gg*, gas-gland; *int*, intestine; *k*, kidney; *pl* and *pv*, positions of pectoral and pelvic fins; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *rsb*, regressed swimbladder; *st*, stomach. (A, ×7·5; B, ×5·4; C, ×15.)

Ichthyococcus ovatus (Cocco) (Text-fig. 6)

St. 1590, 24° 10·4′ N., 17° 18′ W., 13. x. 35, TYFB, 400–320 m. Standard length 34 mm. (7·0 × 2·5 mm.).

While much of the structure could be seen, the swimbladder of this fish was much distorted.

A single rete (length 2·0 mm.) enters the posterior end of the sac to supply a gas-gland (with one median lobe and two lateral lobes) lying on the floor of the sac. Immediately in front of the gland

is part of the resorbent system, which receives two arteries from the by-pass branch of the retial artery. The curious lateral projection of the swimbladder shown in Text-fig. 6 is undoubtedly due to distortion. This is probably the roof of the posterior part of the sac, the part that fits closely within the recess formed by the kidneys.

This projection contained the other part of the resorbent capillary system, for it is supplied from a third branch of the by-pass artery and receives branches from periglandular veins. However, the full appreciation of the circulatory system must be left until a better preserved specimen is available.
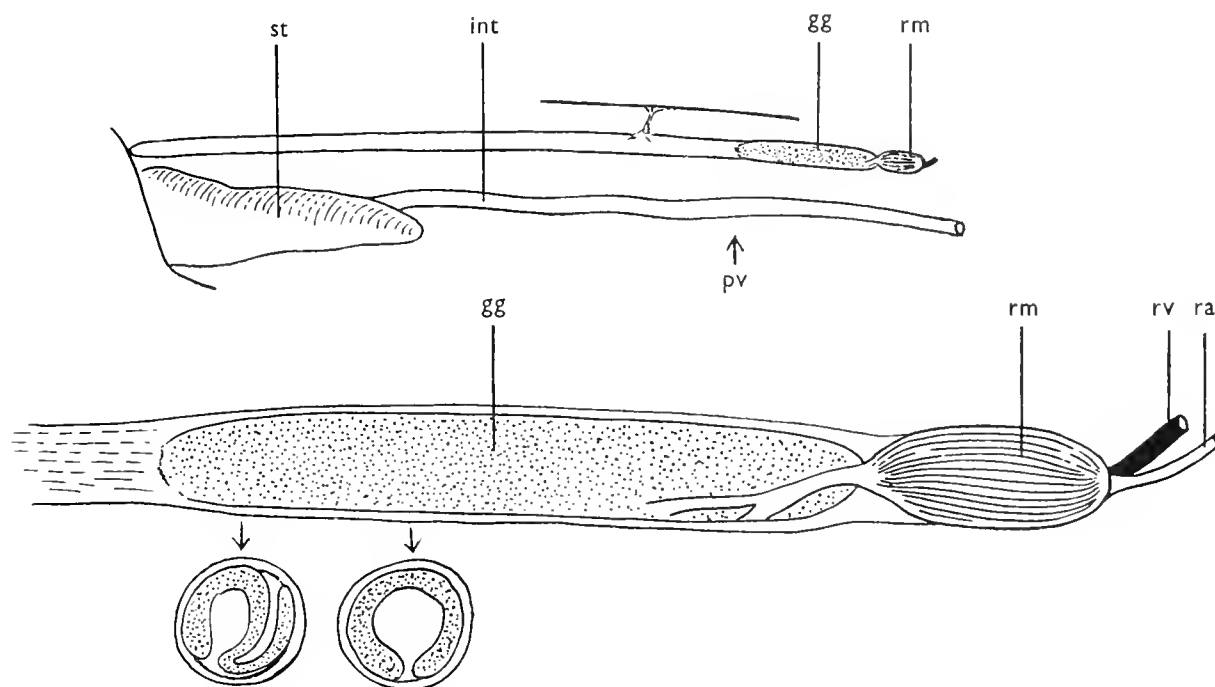
Text-fig. 5. Swimbladder of *Photichthys argenteus* (lateral views). Above, general view; below, posterior part of swimbladder, also showing the appearance of the gas-gland in transverse sections. *gg*, gas-gland; *int*, intestine; *pv*, origin of pelvic fins; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *st*, stomach. (Top figure, × 2·4; bottom figure, × 12.)

Cyclothone Goode & Bean

In *Cyclothone* the swimbladder regresses after metamorphosis into the adult form and becomes invested with fat, which is deposited between the tunica externa and peritoneum of the larval organ.

As the peritoneum may be regarded as forming the outermost layer of the swimbladder wall (see Fänge, 1953), and as, in *Cyclothone*, it completely surrounds the fat and the regressed tissues, this entire structure will be called a swimbladder in the description that follows.

Cyclothone signata Garman (Text-fig. 7 C–E)

Dana St. 7735, 29. vi. 51, 58° 20′ N., 10° 00′ W., 1500-m. wire. Standard length 31 mm.

The swimbladder of this fish lies just in front of the posterior part of the kidney, the backward end reaching a little beyond the points of insertion of the pelvic fins. In side view the organ is elliptical in shape, having a length of about 3 mm. and a median depth of rather less than 1 mm. Except for the postero-ventral part, it is covered with black peritoneum, which also covers a tubular backward extension running under the bulbous terminal segment[1] of the kidney.

This backward extension contains an artery and vein, which enter the rear part of the swimbladder and then divide into a number of smaller vessels. These are bound together in a long rete mirabile

[1] This is largely formed by the Stannius body (Owen, 1938).

having a length of at least 5 mm. After taking a twisting course through loose connective tissues, the rete enters a heart-shaped gas-gland set in the anterior floor of the bladder. This gas-gland is relatively large, with a length of 1·4 mm. and a width of 1·3 mm. and with the glandular tissue arranged in numerous lacunae. The swimbladder has thick walls consisting mainly of loosely woven connective tissues formed within a viscid matrix. There was no investment of fat and this is unlikely to have disappeared through leaching action, for the fish was preserved in formalin. However, Dr Aughtry, who has studied the ecology of *Cyclothone signata* in the Monterey area, California, has written to me of his finding a fat-charged swimbladder in fishes from 27·0 to 35·0 mm. in standard length.
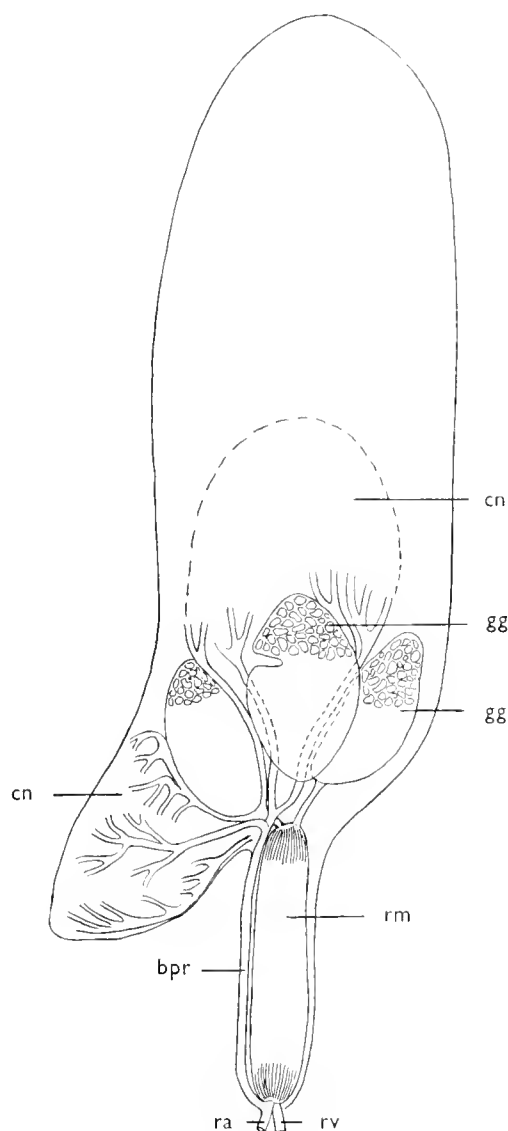
Text-fig. 6. Swimbladder of *Ichthyococcus ovatus*, viewed from above. The three lobes of the gas-gland are on the floor of the sac. *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (× 16.)

Cyclothone braueri Jespersen & Tåning (Text-fig. 8)

St. 287, 2° 49′ 30″ S., 9° 25′ 30″ W., 19. viii. 27, TYF, 850(–o) m. Standard lengths of two individuals examined, 33 and 31 mm.

St. 3094, 44° 20′ N., 16° 49′ W., 21. v. 54, TYFH, 1500(–o) m. Standard length 26·5 mm.

The swimbladder lies well back in the body cavity, the posterior end being above the base of the pelvic fins and immediately in front of the bulbous part of the kidneys. In the 31-mm. fish the organ

is 3 mm. in length and is invested with reticular connective tissue charged with fat droplets. Two blood-vessels, which are closely bound together, enter the posterior under-surface and run forward to a spherical whitish body set in the middle of the fatty tissue. This body has a diameter of 0·6 mm. and within it are the regressed gas-gland and capillaries of the rete mirabile, these being enveloped by a fibrous coat and bound together with more diffuse connective tissues.
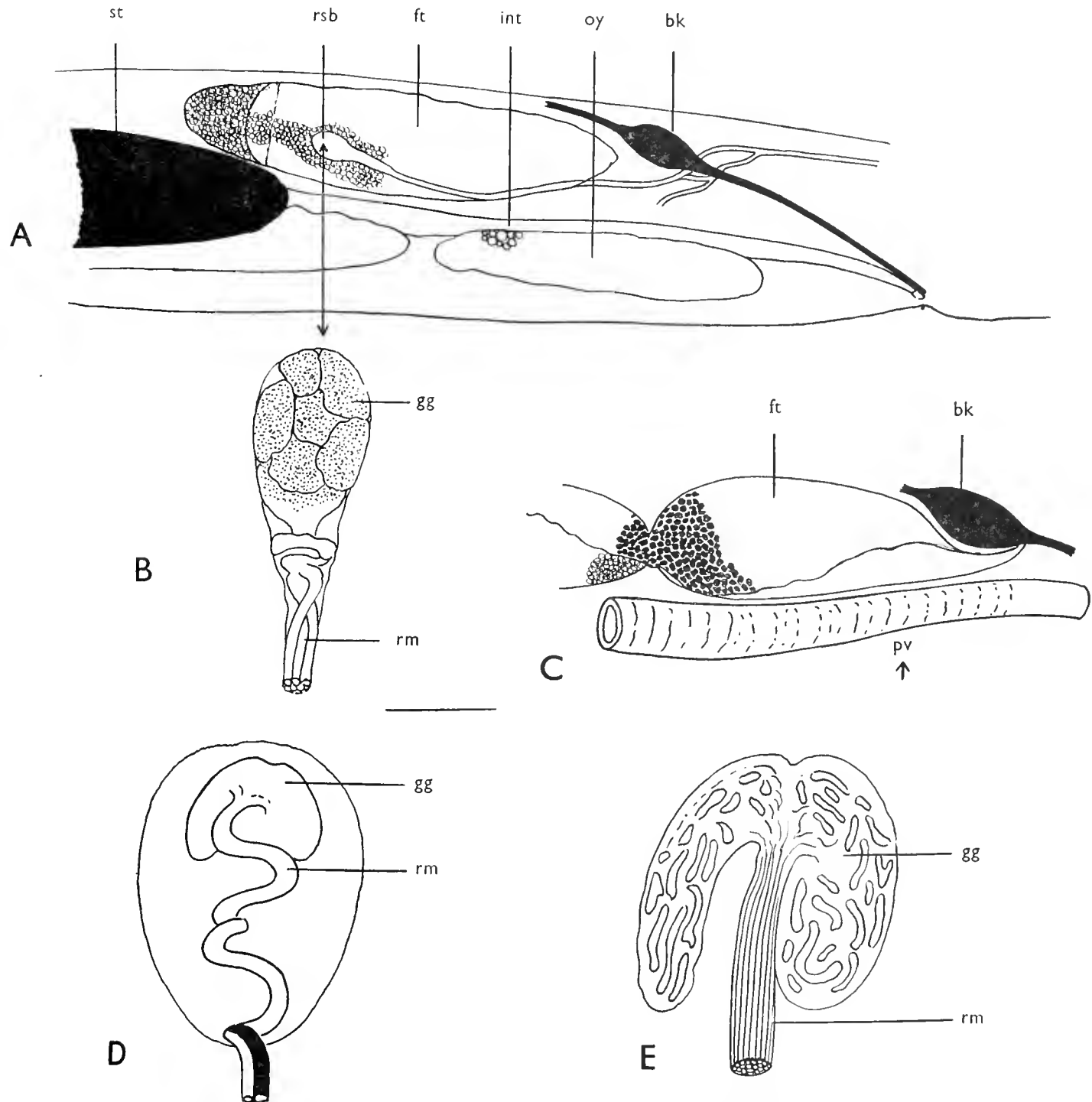
Text-fig. 7. Fat-invested swimbladders of *Cyclothone microdon* (A and B) and *C. signata* (C, D and E). (A and C, lateral views; D and E, ventral views.) *bk*, bulbous, posterior part of kidney; *gg*, gas-gland; *ft*, fatty investment of regressed swimbladder; *int*, intestine; *oy*, ovary; *pv*, origin of pelvic fins; *rm*, rete mirabile; *rsb*, regressed swimbladder; *st*, stomach. (A, × 13·5; B, × 37·5; C, × 18·9; D, × 18·9; E, × 30.)

In the 33-mm. fish the lumen of the sac was not entirely obliterated and the investment of fat was relatively less voluminous, there being a padding of this tissue at the front and rear parts of the sac. On the floor of the sac was a regressed gas-gland. The artery to this structure was traced backwards to the dorsal aorta, while the vein runs to the bulbous part of the kidney, where it may join the renal venous system.

The 26·5-mm. fish has no fatty investment (and it is preserved in formalin) the thick-walled sac measuring about 3 mm. in length. There is a heart-shaped gas-gland on the floor of the anterior half and this receives a long rete mirabile (about 3·5 mm. in length) which enters the posterior end of the organ. The microscopic structure of this swimbladder will be described in a later section (p. 66).
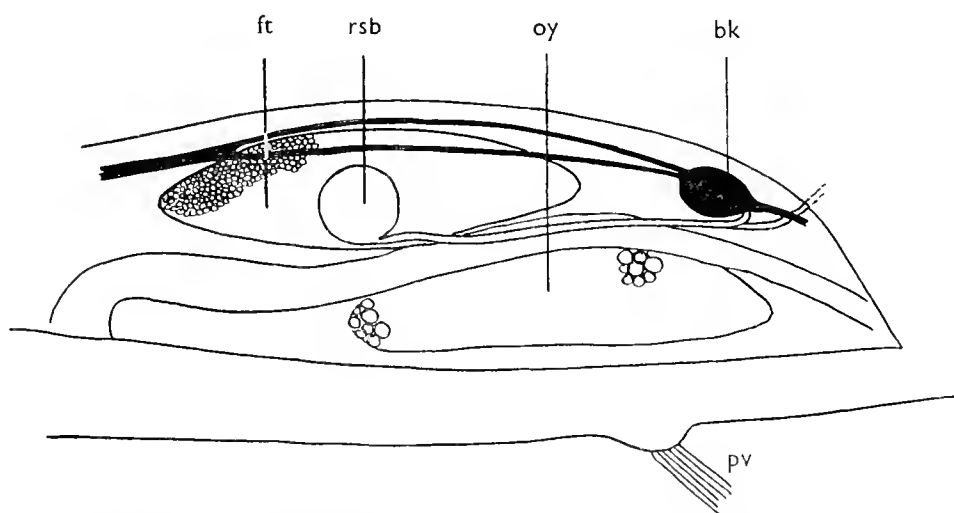
Text-fig. 8. Fat-invested swimbladder of *Cyclothone braueri*. *bk*, bulbous, posterior part of kidney; *ft*, fatty investment of regressed swimbladder; *oy*, ovary; *pv*, pelvic fin; *rsb*, regressed swimbladder. (× 18·9.)

As the larvae of *Cyclothone braueri* have a gas-filled swimbladder, it is clear, as previously mentioned, that the organ gradually regresses and receives a thick coating of fat during the adult phase.

Nusbaum-Hilarowicz (1920) studied the histology of the swimbladder of a species of *Cyclothone*, under the name *C. signata*, but in view of Jespersen's and Tåning's (1926) critical work, the species is most likely to be *C. braueri*. The figures and description show that the swimbladder of this fish was in much the same developmental phase as the 26·5 mm. individual described above.

Cyclothone livida Brauer

St. 3094, 44° 20′ N., 16° 49′ W., 21. v. 54, TYFH, 1500(–o) m. Standard length of two fishes examined 55 and 37 mm.

In both these individuals the swimbladder has much the same position in the body-cavity as that of *C. braueri*. It is sausage-shaped, having a length of about 5 mm. in the larger fish and about 4 mm. in the smaller one. The middle diameter in both is about 1·5 mm.

Under the layer of black peritoneum that invests the swimbladder come the silvery or faintly golden globules of the fatty tissue. This entirely fills the swimbladder and, as in *C. braueri*, the fat droplets are held in a rather wide meshed reticular connective tissue. In the middle of the swimbladder is a cream-coloured body receiving blood-vessels entering the posterior end of the organ.

The swimbladder of the larger fish was taken for transverse sectioning and the following extra details of structure seen. At its posterior entry and for most of its course to the regressed gas-gland, the blood system consists of six small vessels bound closely together. Three arterioles each have an

associated venule. Close to the gas-gland there are twelve vessels formed no doubt by the forking of each of the six vessels. The twelve vessels continue into the pear-shaped mass of the gas-gland.

Besides these two fishes, dissection of several other smaller individuals has revealed transition stages between the gas-producing swimbladder of the larvae and the fat-invested structure of the adult (see p. 66).

The microscopic structure of the swimbladder of the 55-mm. fish will be described in a later section (pp. 66–67).

Cyclothone microdon (Günther) (Text-fig. 7 A, B)

St. 239, 46° 56′ 00″ S., 46° 03′ 00″ W., 2. vi. 27, N 450, 1350–1050(–0) m. Standard length of fish 52 mm.

As in other adult *Cyclothone*, the fat-invested swimbladder of *C. microdon* is slung in the rear part of the body-cavity, the backward end lying just before the enlarged posterior part of the kidneys.

In the middle of the blimp-shaped mass of fatty tissue is a small pear-shaped, cream-coloured body, receiving blood-vessels that enter the posterior under-surface of the organ. A vein, which may be an extension of the renal venous complex, runs forward from the bulbous posterior part of the kidney. The origin of the artery that runs side by side with it could not be traced with certainty. After entering the swimbladder these two vessels continue forward within the fatty tissue and spiral round each other just before entering the pear-shaped structure. This consists of regressed glandular cells and associated capillaries, which are invested and bound together with connective tissues. In the above fish this structure measured 0·75 mm. in length and 0·3 mm. in greatest width, while in another individual of the same size the length was 0·4 mm.

Cyclothone acclinidens Garman

John Murray Expedition, St. 95 Arabian Sea, 2-m. tow-net, 1400-m. wire. B.M. Reg. no. 1939.5.24. 115–250. Standard length of fish 30 mm.

The swimbladder of this species has a very similar structure to that in the four species just described,

Family STERNOPTYCHIDAE

Argyropelecus aculeatus Cuvier & Valenciennes (Text-fig. 9)

St. 257, 35° 01′ 00″ S., 10° 18′ 00″ E., 24. vi. 27, N 100 H, 111 m. B.M. Reg. no. 1930.1.12. 367–8. Standard length 23 mm. (3·5 × 2·5 mm.).

The swimbladder of this hatchet fish is ellipsoidal in form and is slung in the upper part of the body-cavity. At the posterior end of the sac is a massive rete mirabile. It originates at the level of the long axis and extends under the sac over a length of 1·2 mm. Seen from below, the rete is acorn-shaped, the bulbous head consisting of the first division of the artery and vein into finer vessels. These then divide again into the thousands of closely intercalated capillaries that form the rest of this structure.

The gas-gland encircles a heart-shaped capillary bed which extends over the middle region of the swimbladder floor. There are two glandular lobes, each consisting of a band of tissue with expanded posterior and anterior regions (see Text-fig. 9 B).

Arteries and veins leave the front of the rete and run into the gas-gland. There are lateral vessels to the posterior expanded parts of the gland and three central vessels running forwards along the mid-ventral line. The middle vessel is a vein which forks to send a branch to each of the anterior expanded parts. On either side of the vein is an artery, each of which follows the bifurcations to the gas-gland.

The arterial supply to the capillary network comes from the artery to the rete mirabile, which sends off a branch just before its point of entry. This branch runs forwards along the right side of

the rete and then forks into two sub-branches (see Text-fig. 9B) serving the left and right halves of the capillary area. Each sub-branch gives off arterioles dividing to form capillaries. The venous part of the capillary circulation comes from the glandular veins from branches running along the inner edges of the two lobes. These branches break up into venules and capillaries that join the arterial complex. The capillary arterial stream is thus by-passed round the rete mirabile, but the return venous flow eventually runs through this structure by way of the glandular veins.
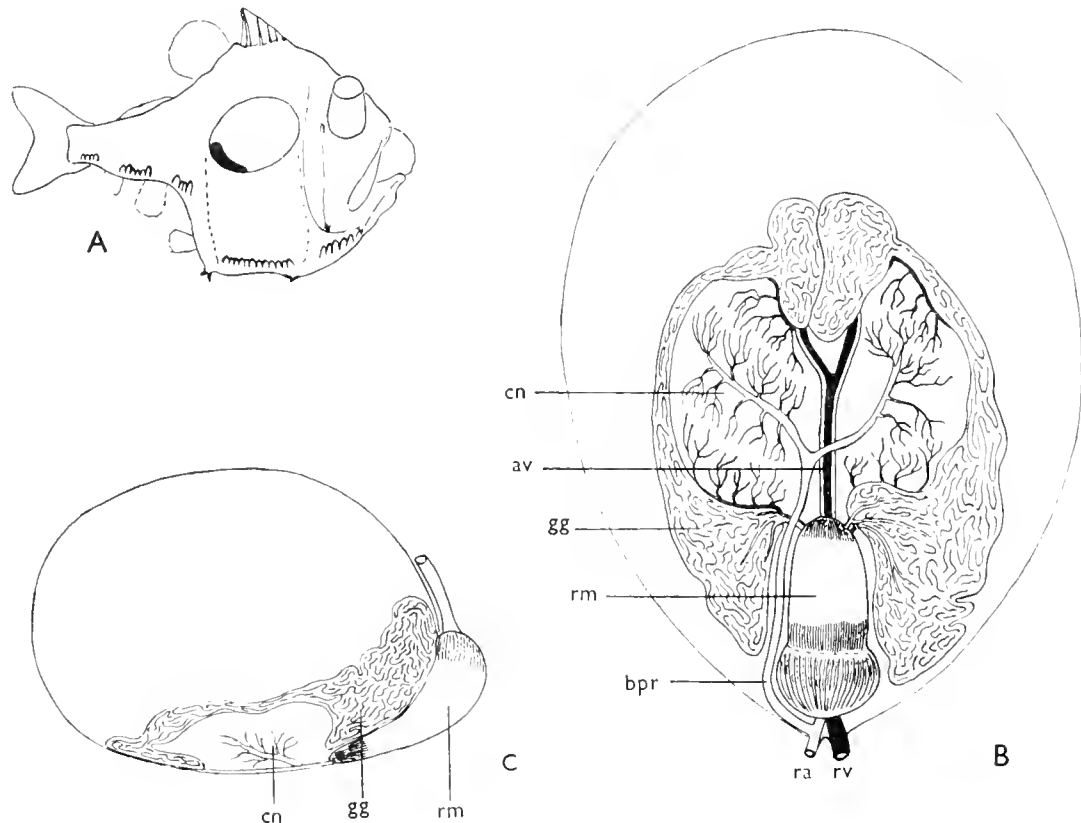
Text-fig. 9. Swimbladder of *Argyropelecus aculeatus*, viewed (A) in position in fish, (B) ventrally, and (C) laterally. Veins shown black, arteries white. *av*, artery-vein association supplying gas-gland; *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (A, × 1; B, × 22·5; C, × 17.)

Argyropelecus olfersii (Cuvier)

Taken by M.V. 'Sarsia' off Concarneau. Standard length 38 mm. (4·5 × 3·0 mm.).

The swimbladder is suspended in the upper half of the body cavity. The sac is oval in outline, and as it is quite relaxed the walls are fairly thick.

A long, club-shaped rete mirabile, with a length of 2·75 mm., enters the posterior end of the sac to supply the gas-gland. An artery from the dorsal aorta and a vein from the cardinal system (between the kidneys) run into the posterior end of the rete.

The gas-gland extends over the roof, side walls and floor of the rear half of the sac, the part over the first two regions appearing to be subdivided into five or six lobes. There is a single lobe on the floor. Each lobe receives an artery and vein from the rete mirabile, while an interglandular capillary network extending over the inner surface of the roof also obtains blood from anterior retial vessels. Longitudinal sections also revealed that there is a capillary network in the floor of the sac (in front of and around the gas-gland). A branch of the retial artery, which subdivides just before entering the rete, runs under the latter and then forwards to break up into capillaries, which run over the inner

surface between the ventral and lateral sections of the gas-gland. The entire capillary circulation, which seems to be much like that of *A. aculeatus*, must form an effective inner surface for the diffusion of gases into the blood.

Argyropelecus sladeni Regan

St. 285, 2° 43′ 30″ S., 00° 56′ 30″ W., 16. viii. 27, N 450 H, 175–125(–0) m. B.M. Reg. no. 1930.1.12. 401–6. Standard length 20 mm. (1·75 × 1·5 mm.).

The swimbladder of this species is almost spherical and lies above the stomach in the upper half of the body cavity.

The single rete mirabile receives an artery from the dorsal aorta and a vein that originates between the kidneys. The retial complex formed from these two vessels is cylindrical and enters the floor of the sac from behind to supply the gas-gland. This covers part of the floor and extends backwards and upwards over the side and rear walls of the sac. Viewed from above through a hole cut in the roof of the sac, vessels leaving the rete can be seen running forwards over the floor to the ventral part of the gland.

The two non-glandular areas on either side of these vessels are invested with a capillary network, which has been described more fully under *A. aculeatus*.

Argyropelecus hemigymnus Cocco

Nusbaum-Hilarowicz (1920) found the swimbladder of this hatchet fish to be dilated anteriorly and narrowed posteriorly. Two ligaments of connective tissue attached to the front part of the sac extend upwards to a fastening on the roof of the body-cavity. The walls are constructed of an outer layer of long fibres (mainly running around the sac), a middle and thick layer of loose connective tissue and an inner epithelial layer which forms the gas-gland. This covers the floor and lateral walls of the forward part of the swimbladder, there being a small, median, ventral lobe and two larger lateral lobes. A single long rete mirabile enters the rear part of the swimbladder and runs forwards under the floor to the gas-gland.

Sternoptyx diaphana Hermann (Text-fig. 10 C, D)

St. 281, 00° 46′ 00″ S., 5° 49′ 15″ E., 12. viii. 27, TYF, 950–850(–0) m. B.M. Reg. no. 1930.1.12. 416–25. Standard length 14 mm. (2·7 × 2·5 mm.).

St. 269, 15° 55′ 00″ S., 10° 35′ 00″ E., 26. vii. 27, TYF, 700–600(–0) m. B.M. Reg. no. 1930.1.12. 413–15. Standard length 39 mm. (9·0 × 5·0 mm.).

The swimbladder is a heart-shaped organ lying in the upper half of the body-cavity. The long axis of the sac, which is thin-walled, is directed downwards and slightly backwards, so making an acute angle with the vertical axis of the fish.

There is a pair of suspensory ligaments running from the roof of the body-cavity to an attachment on the posterior part of the roof of the swimbladder. The other suspensory structures, which are more in the nature of mesenteries, are attached to the anterior middle region and the bottom of the sac. Both taper to points of attachment on the peritoneum of the body-cavity, the former to a point opposite the top of the stomach, and the latter to a point behind the basal part of the intestine.

The single, club-shaped rete mirabile, which has a length of 2 mm. in the larger fish, enters the roof of the swimbladder. It receives a branch from the posterior cardinal vein and an artery (running between the kidneys) from the dorsal aorta. The gas-gland invests the roof and is composed of three lobes, each receiving blood-vessels from the rete mirabile.

The fine structure of the swimbladder of this species has been described by Nusbaum-Hilarowicz (1920). Besides noting the bipolar structure of the rete mirabile, he saw that certain of the outgoing

retial vessels formed a capillary network over the inner surface of the sac between the lobes of the gas-gland.

Polyipnus laternatus Garman (Text-fig. 10A, B)

Position, 13° 25′ N., 18° 22′ W., 28. x. 25, N 450 V, 900(–0) m. B.M. Reg. no. 1930.1.12. 458–67. Standard lengths 32·5 and 26·5 mm.

St. 1582, 05° 39·1′ S., 46° 22·3′ E., 29. v. 35, N 450 H, 1900–1850(–0) m. Standard length 36·0 mm.

The swimbladder of this species is suspended in the upper half of the body-cavity, just above the stomach. The sac is more or less oval in side view, with its long axis parallel to that of the fish. In the three individuals examined (in the order given above) the sac had a length and middle depth of 7·0 and 4 mm., 1·75 and 1·0 mm. and 6·0 and 3·5 mm.
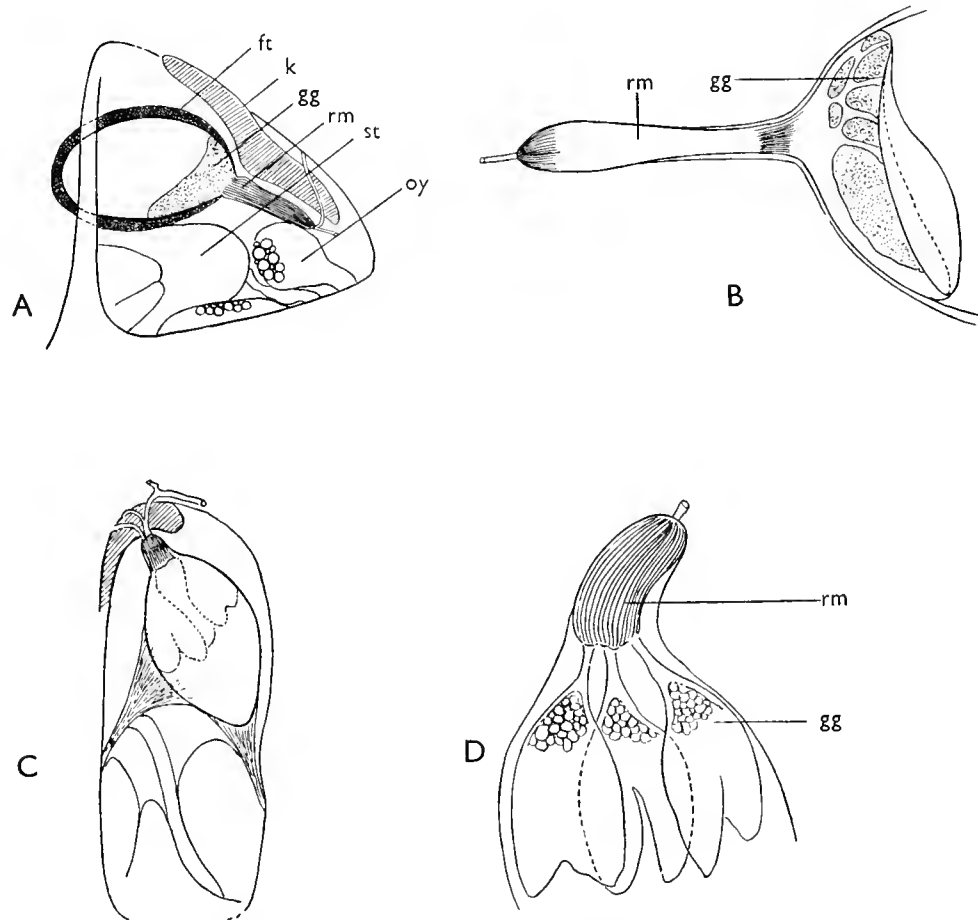
Text-fig. 10. Swimbladders of *Polyipnus laternatus* (A and B) and *Sternoptyx diaphana* (C and D). A and C, lateral views, showing position of swimbladder in body-cavity; C and D, rete mirabile and gas-gland. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *k*, kidney; *oy*, ovary; *rm*, rete mirabile; *st*, stomach. (A, ×3·5; B, ×11·5; C, ×5; D, ×7·5.)

A long club-shaped rete mirabile enters the posterior end of the swimbladder, the measurements of its length in the two largest fishes being about 3·5 mm. The gas-gland lies immediately in front of the rete and is partly or entirely divided into two left and right halves.

A layer of fatty tissue invests the swimbladder walls of the 26·5 and 32·5 mm. fishes. The deposition of the fat takes place between the peritoneal layer surrounding the sac and the tunica externa, transverse sections through the swimbladder of the 36 mm. fish revealing that the space between these two layers is filled with loose reticular connective tissue (see also p. 67). The resorbent capillary circulation has not been closely investigated. However, there is an artery running forward by the

side of the rete mirabile, which is undoubtedly homologous with the artery forming part of the capillary network in other stomiatoids. Sections also reveal that there is a capillary network on the floor of the sac between the lobes of the gas-gland and there also appears to be another network in the roof.

Family ASTRONESTHIDAE

Astronesthes niger Richardson (Text-fig. 11)

Dana St. 1378[III], 200-m. wire. B.M. Reg. no. 1929.1.4. 93. Standard length 41 mm. (5·5 × 2·5 mm.).

The swimbladder of this fish, which is elliptical in profile and has thin walls, is slung above the stomach, the extremities lying over the origins of the pectoral and pelvic fins.

A rod-like rete mirabile (1·5 mm. in length) enters the posterior part of the sac. Its blood supply comes from an artery that runs backwards and then upwards between the kidneys to the dorsal aorta and from a vein joining the cardinal vessel at the front end of the enlarged, rear part of the kidneys.

The gas-gland has two lobes, the left being the larger. This is an elongated band of tissue with an enlarged and rounded posterior part, which lies immediately in front of the rete mirabile and invests the lateral walls of the sac. The right lobe is a triangular patch of tissue lying opposite the tip of the left lobe. The length of this lobe is 1·3 mm. as compared with the 3·2 mm. span of the other one.

Each lobe receives blood-vessels leaving the forward end of the rete. The artery and vein to the right lobe run along the lateral walls of the sac.

The resorbent capillary network, which lies just under the inner epithelium, covers most of the swimbladder roof. The by-pass vessel from the retial artery runs forwards along the right side of the rete and then describes an undulating course about the long axis of the sac. This artery gives off arterioles on either side, which break up into capillaries. The circulation is completed by venules and capillaries that come from vessels running along the upper edges of the gas-gland lobes.

Astronesthes lucifer Gilbert (Text-fig. 12A, B)

B.M. Reg. no. 1922.6.7. 14–23. Misaki, Japan. Standard length 73 mm. (16·5 × 3·5 mm.).

The swimbladder of this astronesthid is an elongated ellipsoid sac tapering to a point anteriorly. Above the base of the pelvic fins and at the posterior end of the organ is a single, bulbous rete mirabile, 2·5 mm. in length and 1·3 mm. in width. This is fed with arterial blood by a vessel that extends backwards and then turns upwards through the kidneys to join the dorsal aorta. The vein enters the kidneys at the point where they begin to enlarge behind the swimbladder.

The two lobes of the gas-gland, which extend over the floor and sides of the swimbladder, come immediately in front of the rete mirabile. Along the upper and lower parts of each lobe are vessels, which lead to the rete.

Astronesthes gemmifer Goode & Bean (Text-fig. 12D)

Westmann Isles, Iceland. B.M. Reg. no. 1950.6.30. 2. Standard length 168 mm. (20 × 3 mm.).

The swimbladder of this species was found over the posterior half of the stomach. It is an elongated organ with very thick walls. At the posterior end of the bladder is a conical rete mirabile measuring about 3·5 mm. in length and 1·5 mm. in greatest width.

The gas-gland appears to be a solid rod-like structure, but actually consists of two closely contiguous lobes which together fill most of the lumen of the sac. All the tissues appear to be very contracted, or it may be that the organ regresses during adult life.
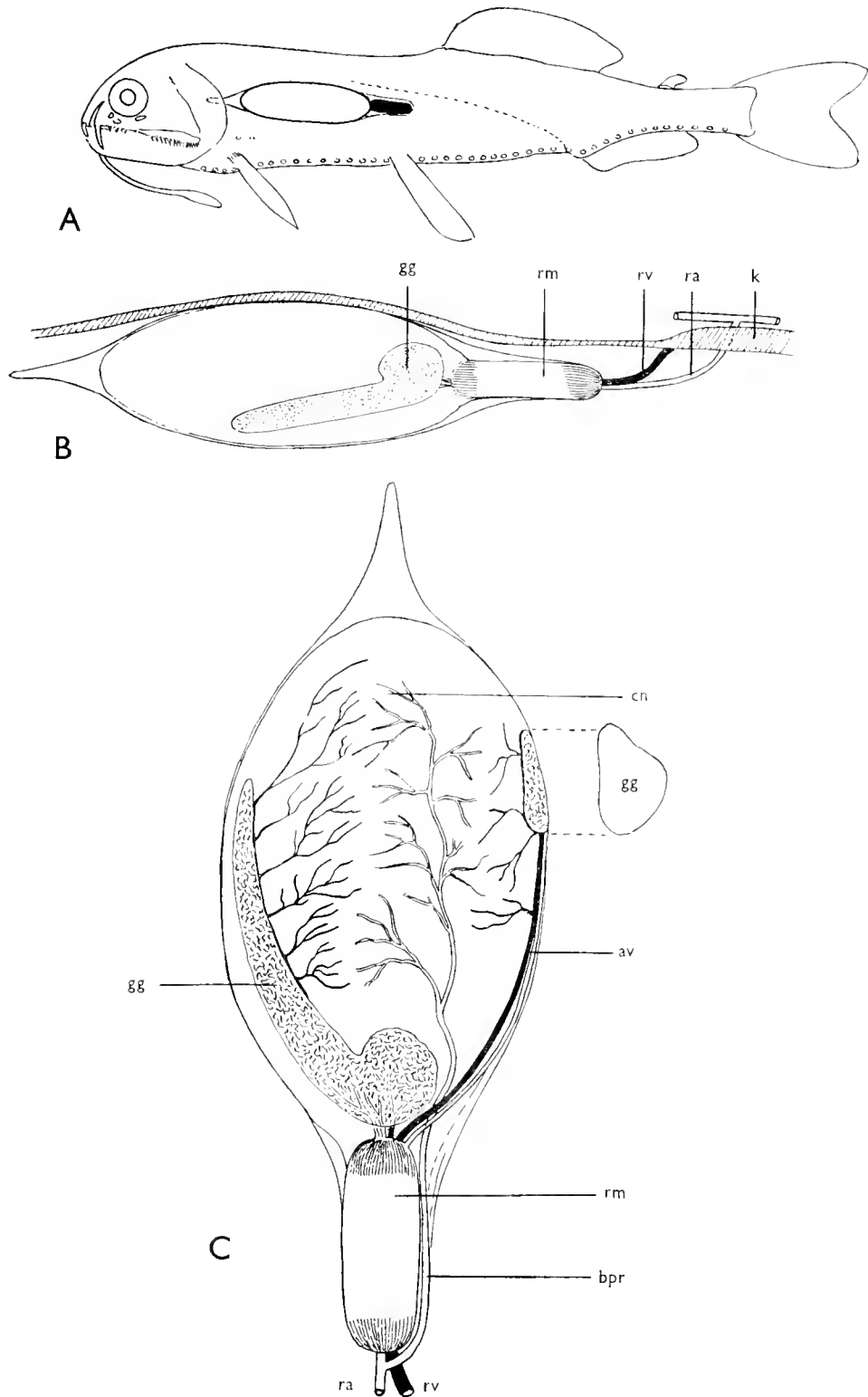
Text-fig. 11. Swimbladder of *Astronesthes niger*, seen (A) in fish; (B) laterally, and (C) ventrally. Veins shown black, arteries white. *av*, artery-vein pair to gas-gland; *bpr*, by-pass branch of retial artery; *gg*, gas-gland; *k*, kidney; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (A, × 2; B, × 8; C, × 12.5.)
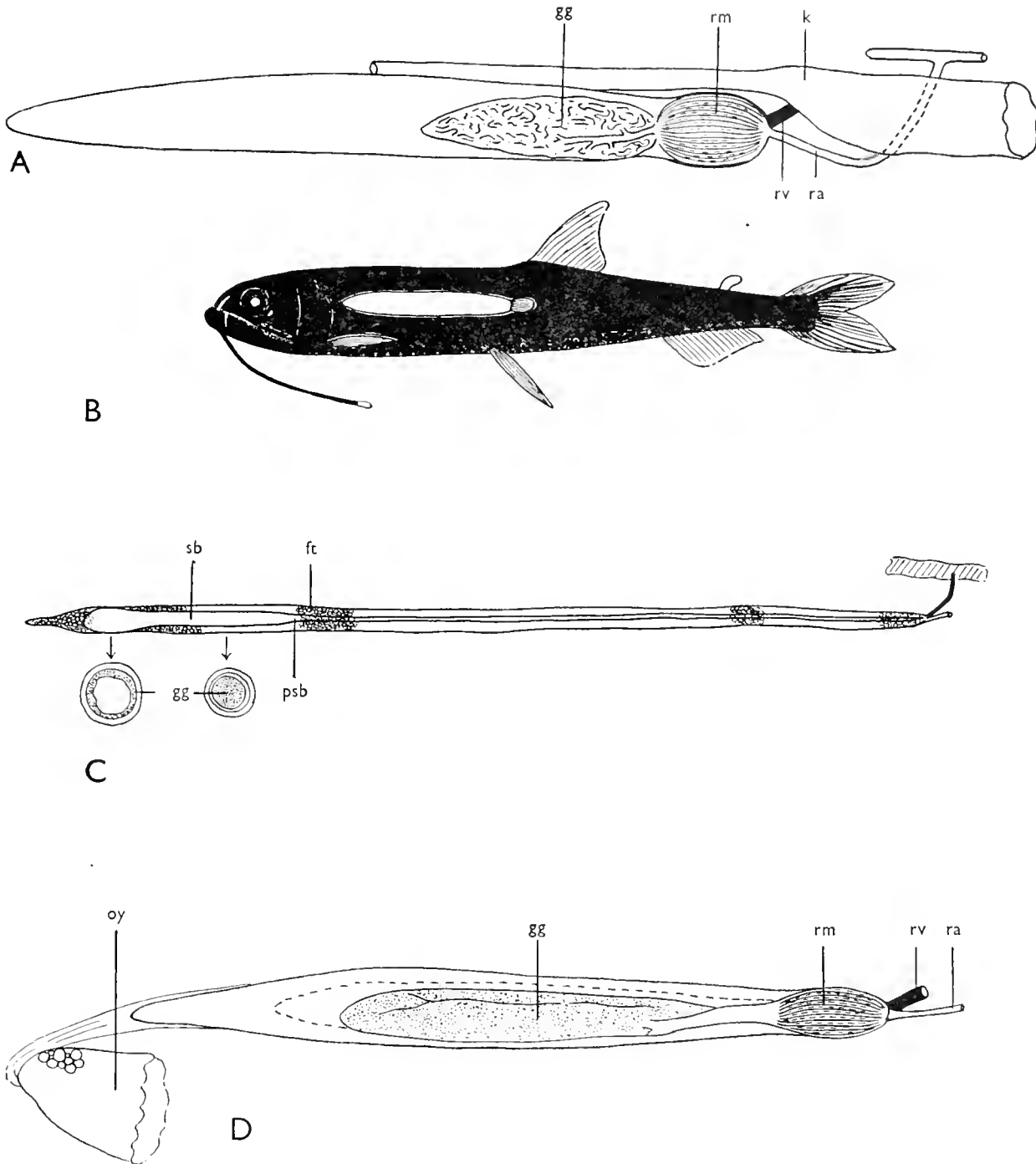
Text-fig. 12. Swimbladders of *Astronesthes lucifer* (A and B); *Borostomias antarcticus* (C) and *Astronesthes gemmifer* (D). Lateral views. In (C) two transverse sections of the swimbladder show the inner disposition of the gas-gland. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *k*, kidney; *oy*, ovary; *psb*, posterior end of swimbladder; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *sb*, swimbladder. (A, × 7·5; B, × 1; C, × 2; D, × 4·8.)

Astronesthes similis Parr

Dana St. 939, 500-m. wire. B.M. Reg. no. 1929.1.4. 81. Standard length 105 mm. (20 × 5 mm.).

The swimbladder bauplan of this species is similar to that of other *Astronesthes* spp. The pointed forward end of the sac, which is thin-walled, lies opposite the posterior edges of the gill covers. There is a bilobed gas-gland immediately in front of the bulbous rete mirabile, which enters the

posterior floor of the swimbladder. The left lobe of the gland is the larger, measuring about 6 mm. in length against the 4 mm. span of the right lobe.

Borostomias antarcticus (Lönnberg) (Text-fig. 12C)

St. 114, 52° 25′ 00″ S., 9° 50′ 00″ E., 12. xi. 26, N 450, 650–700 m. B.M. Reg. no. 1930.1.12. 474. Standard length 167 mm.

The swimbladder of this individual proved to be a tubular structure lying above the anterior part of the stomach. It is club-shaped, measures about 13 mm. in length and contains a regressed gasgland and rete. An artery and vein run into the posterior part of the organ and can be traced back to the backward section of the kidneys. Both the remains of the swimbladder and these blood-vessels are surrounded by a layer of fatty tissue.

Diplolychnus mononema Regan & Trewavas
Standard length 137 mm.

No trace of a swimbladder could be found in this individual.
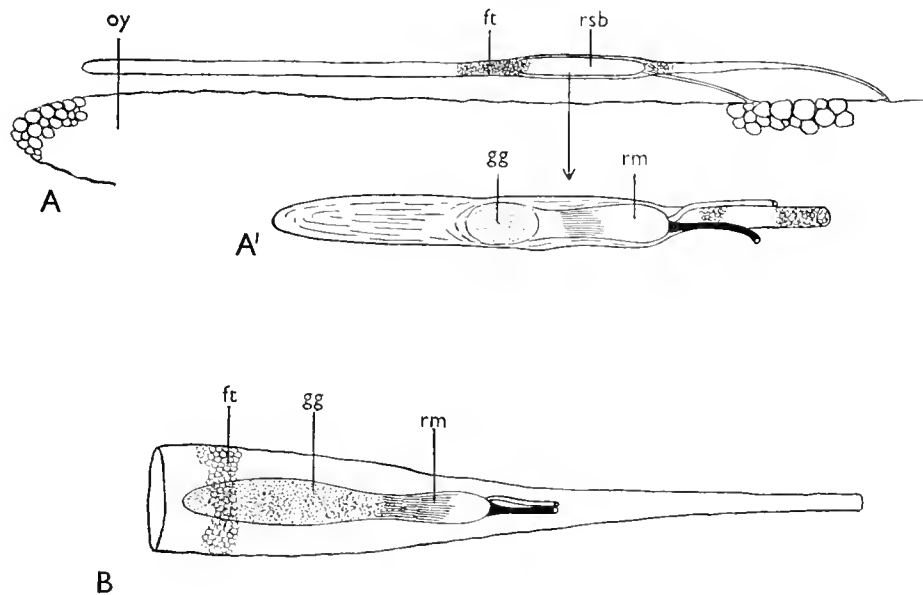
Text-fig. 13. Fat-invested swimbladders of *Stomias affinis* (A and A′) and *S. colubrinus* (B). Lateral views. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *oy*, ovary; *rm*, rete mirabile; *rsb*, regressed swimbladder. (A, × 4·5; A′, × 11·5; B, × 17·5.)

Family STOMIATIDAE

Stomias affinis Günther (Text-fig. 13A)

St. 276, 5° 54′ 00″ S., 11° 19′ 00″ E., 5. viii. 27, TYF, 150(–0) m. B.M. Reg. no. 1930.1.12. 542–3. Standard length 106 mm.

In this individual there is a regressed swimbladder lying above the ovaries. Fatty tissue invests the organ and is continued forwards and backwards into rod-like prolongations. The anterior one extends to the front of the ovary, while the backward one, which is more slender and tapering, ends rather more than half-way down the body-cavity.

The length of the swimbladder is about 4·5 mm. Entering the posterior end is an artery and vein supplying a club-shaped rete mirabila which is about 1·5 mm. in length. In the middle of the bladder is a small gas-gland, 0·8 mm. in length, which all but obliterates the lumen. Forward of the gland there is no lumen, but merely a 'solid' mass of connective tissue.

Stomias colubrinus Garman (Text-fig. 13 B)

Position, 13° 25′ 00″ N., 18° 22′ 00″ W., 28. x. 25, N 450 V, 900(–0) m. Standard length 103 mm.

Beginning above the base of the pectoral fins and running just below the kidneys is a well-defined strand of fatty tissue, with a length about four-fifths that of the body-cavity. Within this tissue, about three-fifths of the way along its length, was found the regressed tissues of the swimbladder. Running forward to a posterior rete mirabile is an artery and vein. The rete leads to solid club-shaped structure which consists of a mass of regressed gland cells invested with connective tissues. The rete and gland were about 2·5 mm. in length.

Stomias ferox Reinhardt

Position, 41° 37′ N., 12° 30′ W., 10. x. 25, N 200 H, 900(–0) m. B.M. Reg. no. 1930.1.12. 541. Standard length of fish 85 mm.

As in *S. affinis* and *S. colubrinus*, there is a well formed strand of fatty tissue, lying just below the kidneys and originating above the base of the pectorals. In the above individual this fat body extended for about 25 mm. down the body-cavity to end in a tapering section attaching to the intestinal mesentery.

No remains of retia mirabilia or gas-gland could be found in this tissue.

Family MELANOSTOMIATIDAE

No swimbladder could be found in adult individuals (judged by the development of the gonads) in each of the following species: *Bathophilus metallicus* Welsh, *B. pawneei* Parr, *Eustomias obscurus* Vaillant, *Echiostoma tanneri* (Gill).

Beebe and Crane (1939) gave an account of the internal organs of a number of species but made no mention of a swimbladder.

Family CHAULIODONTIDAE

Chauliodus sloanei Schneider and C. barbatus Garman

No swimbladder was found in two adult fishes examined.

Family IDIACANTHIDAE

Idiacanthus fasciola Peters

No swimbladder was found in adult specimens.

Family MALACOSTEIDAE

No trace of a swimbladder could be found in adult *Malacosteus niger* Ayres and *Photostomias guernei* Collett.

Suborder SALMONOIDEA

Family OPISTHOPROCTIDAE

Opisthoproctus soleatus Vaillant (Text-fig. 14 D)

St. 3484, 39° 55′ N., 20° 01′ W., 1. x. 56, IKMT, 750(–0) m. Standard length 35 mm. (6·5 × 2·5 mm.).

The swimbladder of *Opisthroproctus*, which is ellipsoidal in form, lies above the stomach. When fully expanded it is evidently no less capacious an internal float than the swimbladder of a myctophid (of the same size).

Two blood-vessels enter the anterior end of the sac and then subdivide to form about twelve branches, which take more or less parallel courses within the swimbladder wall until they reach the gas-gland. Each of these vascular branches consists of from six to twelve closely associated capillaries, which are arranged in the form of a ribbon. In cross-section the ribbon consists of alternating arterial and venous capillaries (or arterioles and venules), the arterial elements having a diameter of about 12μ while the venous ones measure about 20μ. Clearly these are retial structures (see Text-fig. 14D), but they are quite unlike the massive retia of most teleosts with a closed swimbladder. Such elements might well be called micro-retia mirabilia.

These retia enter the gas-gland without subdividing and form capillary loops within the secretory tissue. The gland occupies a median region and entirely surrounds the sac. Beyond the gas-gland the walls consist of an inner epithelium and outer connective tissues. Perhaps it is here that resorption of gases takes place.

Opisthoproctus grimaldii Zugmayer (Text-fig. 14E)

St. 1746, from 32° 02·1′ S., 87° 02·5′ E. to 31° 56·6′ S., 86° 55·1′ E., 22. iv. 36, D.R.R. 2513 m. Standard length 65 mm. (15·0 × 6·0 mm.).

Opisthoproctus grimaldii has a capacious swimbladder which is rounded anteriorly and tapers to a point at the other extremity. As in *O. soleatus*, blood-vessels enter the forward tip of the sac. There is a large vein that originates between the kidneys (presumably coming from the cardinal vein), while there are two arteries, one being a branch of the mesenteric system, the other running forward from the vessel to the ovaries.

Again, these vessels subdivide to form micro-retia, each composed of a ribbon of closely associated capillaries (from twelve to sixteen). The venous elements have a diameter of from 12 to 16μ, while their arterial counterparts measure from 8 to 10μ. At the forepart of the swimbladder there appeared to be about 30 micro-retia, these running backward to supply glandular patches, which seemed to be less concentrated than those of *O. soleatus*. However, they were most numerous over the middle part of the sac. These patches are formed of cells varying in size from about 30 to 150μ.

Winteria telescopa Brauer (Text-fig. 14A, B)

St. 2066, 04° 56·4′ N., 14° 46·7′ W., 5. v. 37, N 450 B, 1550–0 m. Standard length 100 mm. (5·0 × 2·0 mm.).

The swimbladder of *Winteria* is suspended in the body-cavity just behind the stomach. In the above individual the sac is very relaxed, the walls being thick and having a nacreous appearance. From the posterior end of the swimbladder a long band of connective tissue runs backwards to an attachment on the right ovary.

An artery and vein enter the anterior end of the sac and subdivide into a number of smaller vessels, which run towards the gas-gland. This is found in the posterior half of the sac and seems to be a flattened oval structure lying on the floor of the swimbladder. However, the tissues are so shrunken that this may not be its true form. Running to the glandular area are at least twelve micro-retia composed of from eight to fourteen capillaries.

Macropinna microstoma Chapman

Chapman (1942b) was unable to find a swimbladder in this species.

Family MICROSTOMIDAE

Xenophthalmichthys danae Regan

Bertelsen (1958) records that the swimbladder is absent.

A well-developed swimbladder is found in the genera *Argentina*, *Glossanodon*, *Microstoma* and *Nansenia* (Cohen, 1958; Fänge, 1958, and personal observation). Fänge's description of the swim-bladder of *Argentina silus* shows that micro-retia are also present in another deep-sea salmonoid and that the system is highly developed. I have also found an extensive development of micro-retia in *Microstoma* and *Nansenia*. However, as these four genera appear to consist of benthic fishes they are not considered here. Further discussion may be found in the section on pages 53-54.

The swimbladders of the two species of *Opisthoproctus* and *Winteria telescopa* were not sufficiently well preserved to trace the resorbent capillary network. However, it is likely to be found at the posterior end of the sac. This is certainly true of *Argentina* and *Microstoma*, in which this part is thin walled and carries a capillary bed (see also pp. 79–80).
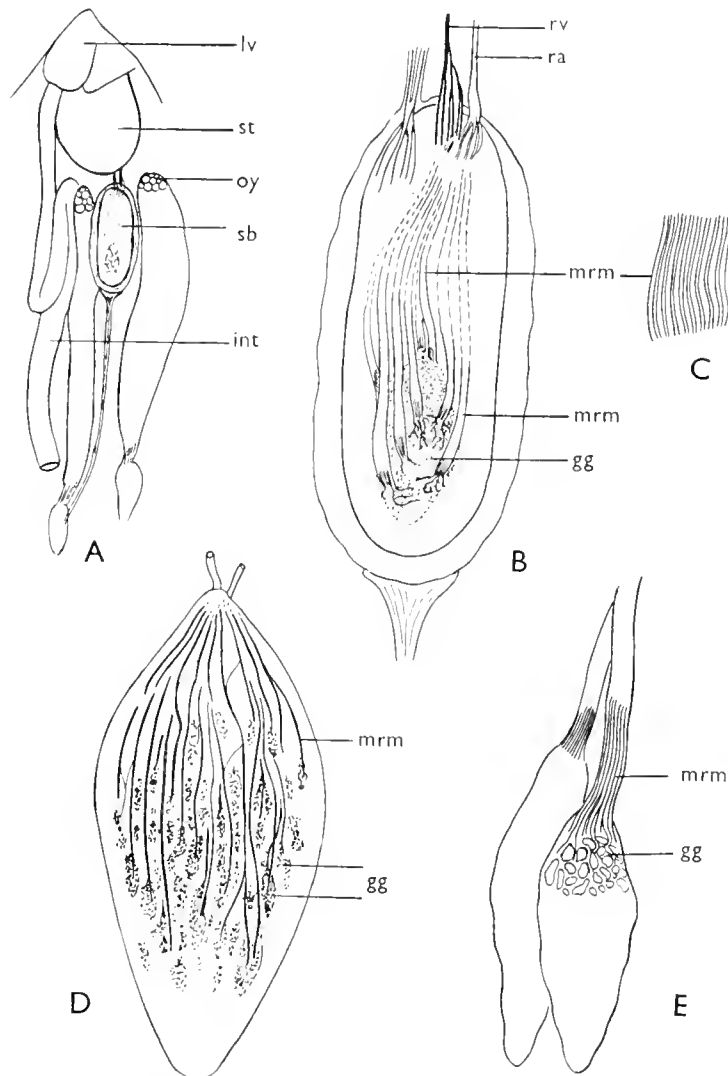
Text-fig. 14. Swimbladders of *Winteria telescopa* (A and B) and *Opisthoproctus soleatus* (D), seen from below. In (C) part of a micro-rete of *Winteria* is seen and in (E) two micro-retia of *Opisthoproctus grimaldii*, which supply patches of gas-gland. *gg*, gas-gland; *int*, intestine; *lv*, liver; *mrm*, micro-rete mirabile; *oy*, ovary; *ra*, retial artery; *rv*, retial vein; *sb*, swimbladder; *st*, stomach. (A, ×3·5; B, ×12·5; C, ×60; D, ×10; E, ×60.)

Family BATHYLAGIDAE

In his synopsis of this family, Chapman (1943) recorded that the swimbladder is completely absent. Beebe (1933), who examined the internal organs of *Bathylagus benedicti* and *B. glacialis*, made no mention of this organ, while I could find no trace of it in *B. antarcticus* and *B. argyrogaster*.

Suborder CLUPEOIDEA

Family ALEPOCEPHALIDAE

Alcock (1899) stated that the Alepocephalidae have no swimbladder. Beebe (1933) examined the internal organs of *Bathytroctes rostratus* and *Xenodermichthys copei*, but made no mention of a swimbladder. I was unable to find any trace of this organ in an adult of the latter species, nor in *Searsia koefoedi*.

Order *INIOMI*

Suborder MYCTOPHOIDEA

Family MYCTOPHIDAE

Myctophum punctatum Rafinesque (Text-fig. 15 A–C)

St. 3233, 46° 02′ N., 09° 19′ W., NH, 0 m. Standard lengths of fishes 74·5, 71·0, 69·0 and 59·0 mm.

In this lantern fish a capacious swimbladder is found above the stomach. The anterior end is opposite the margins of the gill-covers, while the posterior extremity lies under the origin of the dorsal fin. The sac is thin-walled and ellipsoidal in form, the major and minor axis measuring 11·0 and 4·5 mm. in the 69·0-mm. fish.

Three retia mirabilia are found on the underside of the forward, rounded end of the sac. The retial blood supply comes from an artery running backwards and downwards from the dorsal aorta and returns through a vein that joins the hepatic portal system.

In the 74·5-mm. fish, each of the three retia mirabilia (which have a length of about 2 mm.) runs to a corresponding lobe of the gas-gland. The middle lobe is shaped rather like a rose petal and lies over the floor, while the left and right lobes, which are fan-like, extend over the lateral walls. As in all lantern fishes, the surface of the gland has a convoluted appearance, due to the meanderings of the capillary loops with their associated investments of gland cells. This kind of rete in which the arterial and venous capillaries run straight to the gas-gland without forming larger vessels is termed unipolar.

Above the retia mirabilia is a resorbent 'oval' which is partly expanded. It measured 2·5 mm. along the longitudinal axis and 2·2 mm. in width. The oval bears a fine-meshed network of capillaries fed by two branches of the retial artery. The venous return is through a large vessel running upwards and forwards to a point between the kidneys, presumably to the posterior cardinal vein.

In the 69-mm. fish the oval is partly expanded and the opening into the swimbladder has a diameter of 2·5 mm. The capillary-bearing tissue is an egg-shaped blister measuring 3·5 along the longitudinal axis and 3·0 mm. in greatest width. The oval of the 59-mm. fish is shut, the inner surfaces of the walls being thrown into folds. The fine structure of the oval in the closed phase will be dealt with in more detail in a later section (p. 80).

Diaphus rafinesquei (Cocco) (Text-fig. 15 D, E)

St. 3484, 39° 55′ N., 20° 01′ W., 1. x. 56, IKMT, 750(–0) m. Standard length 70 mm.

A detailed description of the swimbladder of this myctophid has been given by Rauther (1922). According to his reconstruction of transverse sections (shown in his fig. 13), the swimbladder of his fish measured about 7 mm. in total length. The middle depth was rather less than 1 mm. In the Discovery fish the length of the sac is about 20 mm. and the middle depth about 7 mm. Rauther showed the walls of the swimbladder to be relatively thick, but the sac was clearly not in an expanded condition. There was an outer fibrous layer which did not cover the roof, and then came two layers of loose and closely packed connective tissue fibres.

Continuing Rauther's description, the inner epithelial layer forms an extensive gas-gland covering most of the floor and side walls of the swimbladder, and also the roof of the anterior part. There are three retia mirabilia supplied by an artery that joins the dorsal aorta close to the coeliac artery, while the venous return is through a vessel opening into the portal system. The left rete extends upwards to the roofing part of the gas-gland, while the middle and right retia supply the remaining glandular area. Measured from Rauther's fig. 13 the lengths of the retia, in the order just mentioned, are about 2·5–3·0 mm.
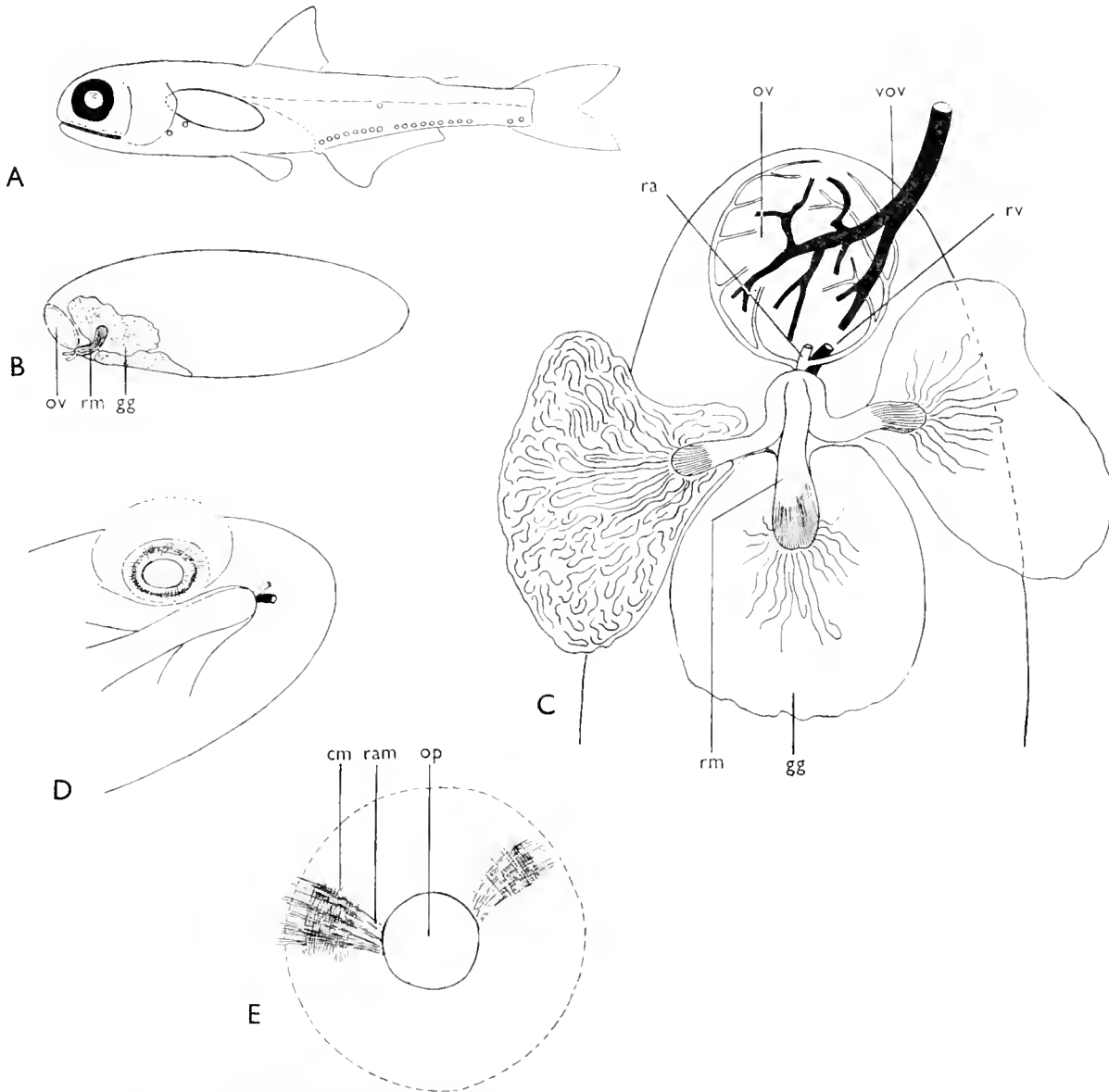
Text-fig. 15. Swimbladder of *Myctophum punctatum*, seen (A) in position in body-cavity of fish, (B) laterally, (C) ventrally (anterior part of organ). The oval of *Diaphus rafinesquei* is shown in Text-figs. 15 D and E. *cm*, circular muscle of oval; *ram*, radial muscle of oval; *gg*, gas-gland; *op*, opening from oval into swimbladder chamber; *ov*, oval; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *vov*, vein to oval. Veins shown black, arteries white. (A, × 1; B, × 5; C, × 12; D, × 7; E, × 15.)

There is an anterior chamber, called by Rauther the praevesica, opening into the right side of the main sac just behind its forward tip. The chamber has an outer fibrous layer and an inner much-folded layer of loose connective tissue containing a capillary network. Rauther remarked that this blood-system was like that he found in the respiratory part of the swimbladder of the mud-minnow,

Umbra. The arterial supply for the network comes from the retial artery, while there is a vein running forward and upwards from the chamber to the cardinal (?) vein.

Examination of the Discovery fish revealed that Rauther's 'praevesica' is no more than a very distorted oval. In this fish the oval lies immediately to the right of the retia mirabilia and the capillary bearing surface is blown out in the form of a blister, due no doubt to the release of pressure as the fish was hauled to the surface. Had sections been cut of this structure, it would also have looked like an anterior chamber. At the base of the oval is a circular aperture with a diameter of about 0·75 mm. which opens into the main cavity. From the rim of this opening radial muscles extend outwards and are crossed by a complex of circular muscle fibres. Clearly the whole structure conforms to that of the oval found in some fishes with a closed swimbladder, much like that described in the perch (*Perca fluviatilis*) by Saupe (1939).

Like *Myctophum punctatum* and *Diaphus rafinesquei*, each of the other lantern fishes dissected has an ellipsoidal swimbladder provided with three unipolar retia mirabilia. The gas-gland is three-lobed, each lobe receiving a corresponding rete. An oval is also present.[1] In view of this, the descriptions which follow will be confined to the more significant features. Immediately after the length of the fish, measurements of the major and minor axes of the swimbladder appear in parenthesis.

Electrona tenisoni (Norman) (Text-fig. 16 D–F)

St. 2023, 50° 17·7′ S., 00° 23·1′ E., 28. iii. 37, N 100 B, 750–400(–0) m. B.M. Reg. no. 1948. 5.14.16. Standard length 47·0 mm. (4·5 × 1·5 mm.).

The swimbladder of this fish is well developed, although this is hardly revealed by the dimensions of the sac, which is much contracted. Three retia, almost 2·5 mm. in length, enter the anterior floor to supply a heart-shaped gas-gland. The bunched-up appearance of the gland, which covers much of the floor, also reveals the collapsed state of the organ.

Towards the base of the retia, but more to the right side of the sac, is the oval, with wrinkled outer walls. The inner tissues lining the wall are folded and ridged, and bear a network of blood capillaries. The structure is almost closed, there being but a small opening (about 0·5 mm. in diameter) communicating with the main lumen of the swimbladder. The blood-supply consists of two branches from the retial artery and a large vein, which runs forward and upward to the cardinal vein between the kidneys.

Electrona rissoi (Cocco)

St. 101, 33° 50′ to 34° 13′ S., 16° 04′ to 15° 49′ E., N 450, 400–350(–0) m. B.M. Reg. no. 1930.1.12. 597–8. Standard length 61 mm. (12 × 4 mm.).

This species has a capacious swimbladder occupying about three-quarters the length of the body-cavity. On the right of the sac and just behind the anterior tip is the oval, which receives a large vein and a number of small branches coming from the retial artery. The organ is almost closed, the walls having a much folded appearance. Around the opening into the main cavity of the swimbladder are circular and radial muscles.

Electrona antarctica (Günther) (Text-fig. 16 A–C)

St. 114, 52° 25′ 00″ S., 9° 50′ 00″ E., 12. xi. 26, N 450, 650–700(–0) m. B.M. Reg. no. 1930.1.30. 622–7. Standard lengths of two fishes examined, 26·0 and 59·0 mm.

St. 2535, 52° 40·8′ S., 02° 45·4′ E., 16. i. 39, N 100 B, 1050–0 m. Standard length 36 mm.

In all three fishes the swimbladder is oval in outline and is suspended in the body-cavity over the forward half of the stomach. The sac of the smallest specimen measured a little more than 3 mm. in

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[1] The part of the swimbladder serving for gas-resorption.

length and 3 mm. in greatest width. The retia mirabilia are contained in a conical projection at the anterior end, and they are wound spirally round one another. When opened out, three long retia were revealed, each about 5 mm. in length, these running to a gas-gland covering about three-quarters of the swimbladder floor.
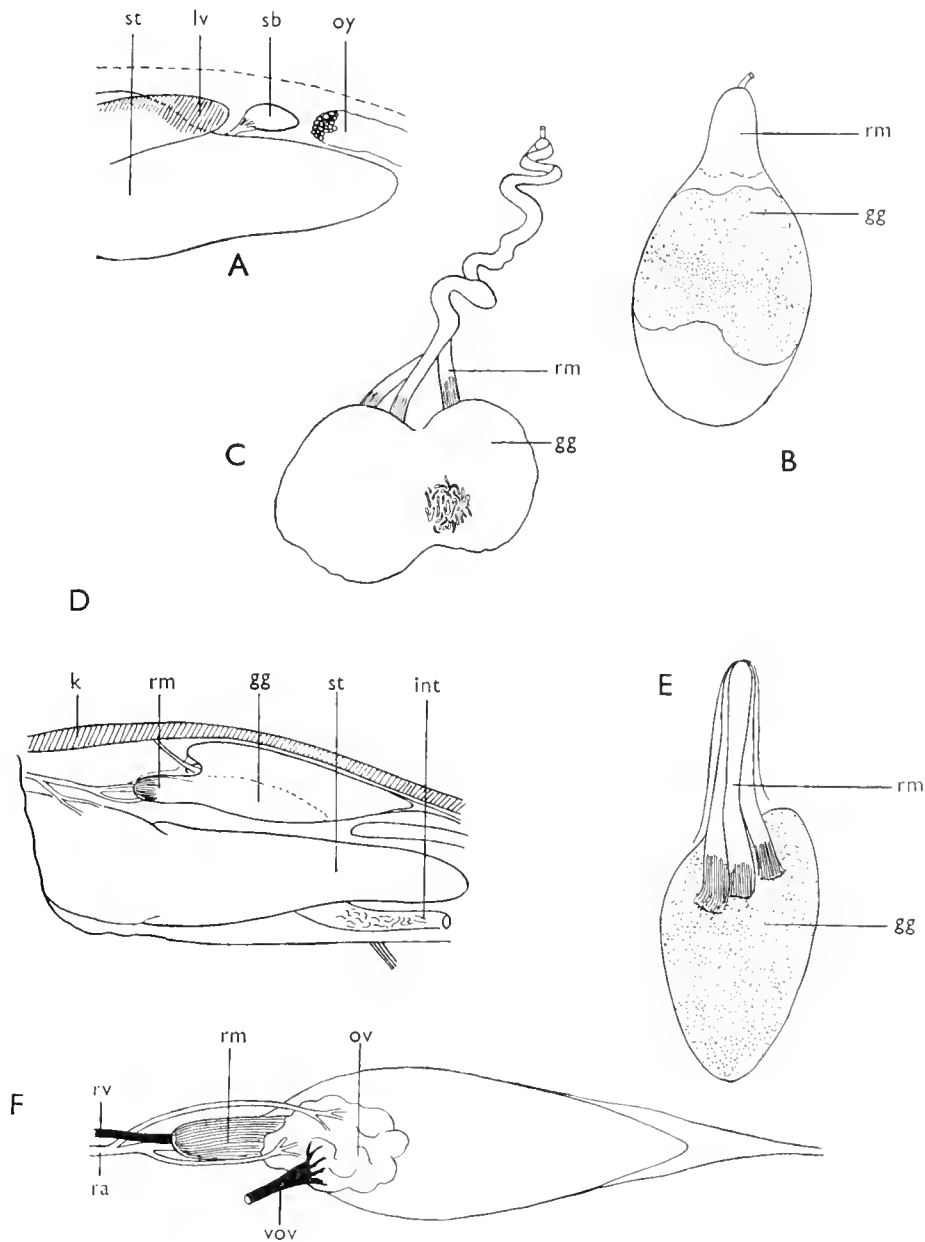
Text-fig. 16. Swimbladders of *Electrona antarctica* (A, B and C) and *E. tenisoni* (D, E and F). B, C, E and F are ventral views. *gg*, gas-gland; *int*, intestine; *k*, kidney; *lv*, liver; *ov*, oval; *oy*, ovary; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *sb*, swimbladder; *st*, stomach; *vov*, vein to oval. (A, × 3·5; B, × 15; C, × 17·5; D, × 6; E, × 18; F, × 14.)

The fish from St. 2535 has a rather larger swimbladder measuring nearly 4 mm. in length. In this, the arterial supply for the retia mirabilia came from the coeliaco-mesenteric vessel. The walls of the bladder were quite thin.

Finally, the swimbladder of the 59-mm. fish measured no more than 2·0 and 1·2 mm. across the major and minor axes. It is clear that the organ regresses during the adult phase.

Hygophum benoiti (Cocco) (Text-fig. 17)

B.M. Reg. no. 85.6.22. 120–9. Straits of Messina. Standard length 4·1 mm. (7·0 × 2·0 mm.).

The swimbladder of this lantern fish is both thin-walled and capacious. At the anterior end three retia mirabilia run into the gas-gland, which covers most of the floor and side walls of the forward half of the organ. Each rete has a length of nearly 3·0 mm.

Over the point of entry of the retia mirabilia into the gas-gland and rather to the right of the swimbladder is a forward conical extension (the distorted oval) receiving a rich supply of blood-vessels. Within the oval the walls are thrown into a series of longitudinal ridges.
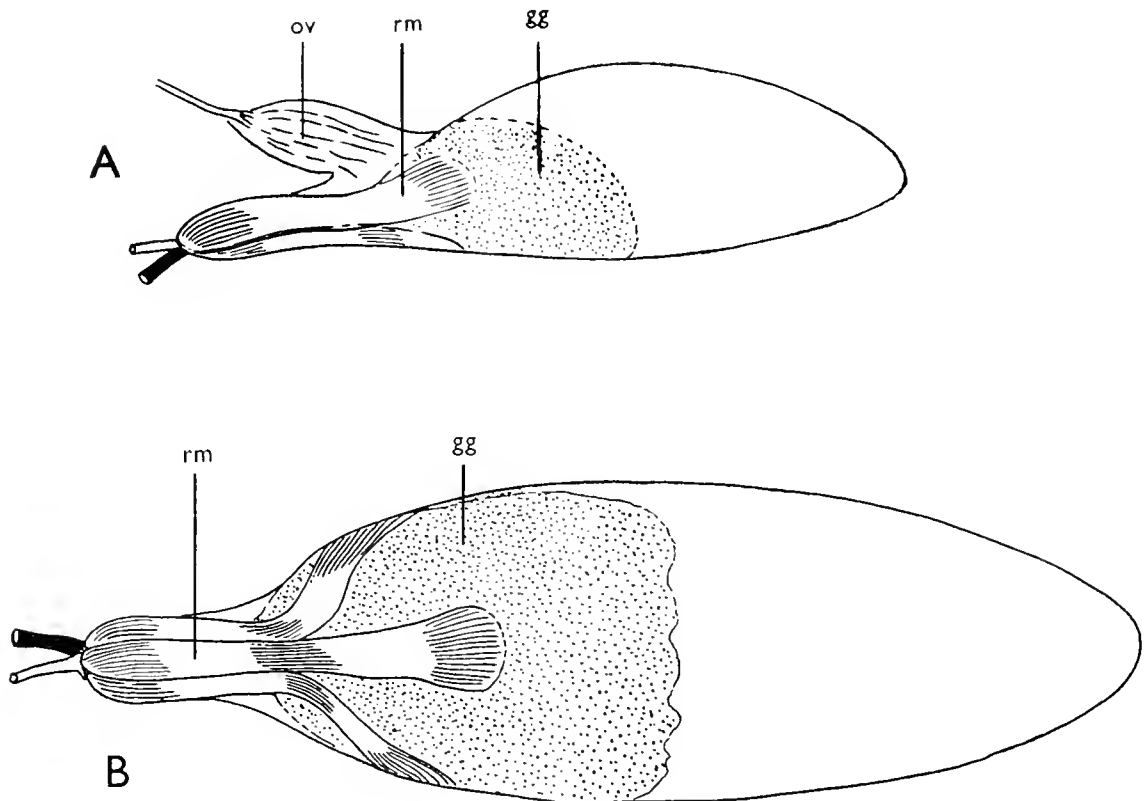
Text-fig. 17. Swimbladder of *Hygophum benoiti*, seen (A) laterally, and (B) ventrally. *gg*, gas-gland; *ov*, oval; *rm*, rete mirabile. (A, × 13·5; B, × 19.)

Benthosema glaciale (Reinhardt) (Text-fig. 18 D–F)

Position, 13° 25′ N., 18° 22′ W., 28. x. 25, N 450 V, 900(–0) m. B.M. Reg. no. 1930.1.12. 641–7. Standard length of fish 45·5 mm. B.M. Reg. no. 1911.2.8. 3–12. Between Faroes and S.W. Ireland. Standard length of fish 58–5 mm.

The swimbladder of this myctophid is thin walled and lies above the stomach. In the 45·5 mm. fish it measured 5·5 mm. in length and about 2 mm. in depth and width at the middle region. A bulbous projection at the fore-end of the bladder contains the three retia mirabilia, which run backwards to a gas-gland investing much of the floor and side walls. Each rete has a mean length of about 3 mm., the two outer systems being rather longer than the middle.

Just behind the base of the bulbous forward projection and on the left-hand side of the swimbladder is a small rounded chamber (the oval) receiving many blood-vessels. The oval has a sphincter-controlled opening into the main cavity, while the walls are thrown into radially disposed folds. In the

Discovery fish the chamber was about 0·5 mm. in diameter and the inner opening, which was oval, measured 0·5 × 0·3 mm. The corresponding figures for the other fish are 0·6 and 0·2 × 0·2 mm.

In both fishes the anterior part of the swimbladder was entirely invested by fatty tissue, which extended under the organ (and beyond it in the larger individual).
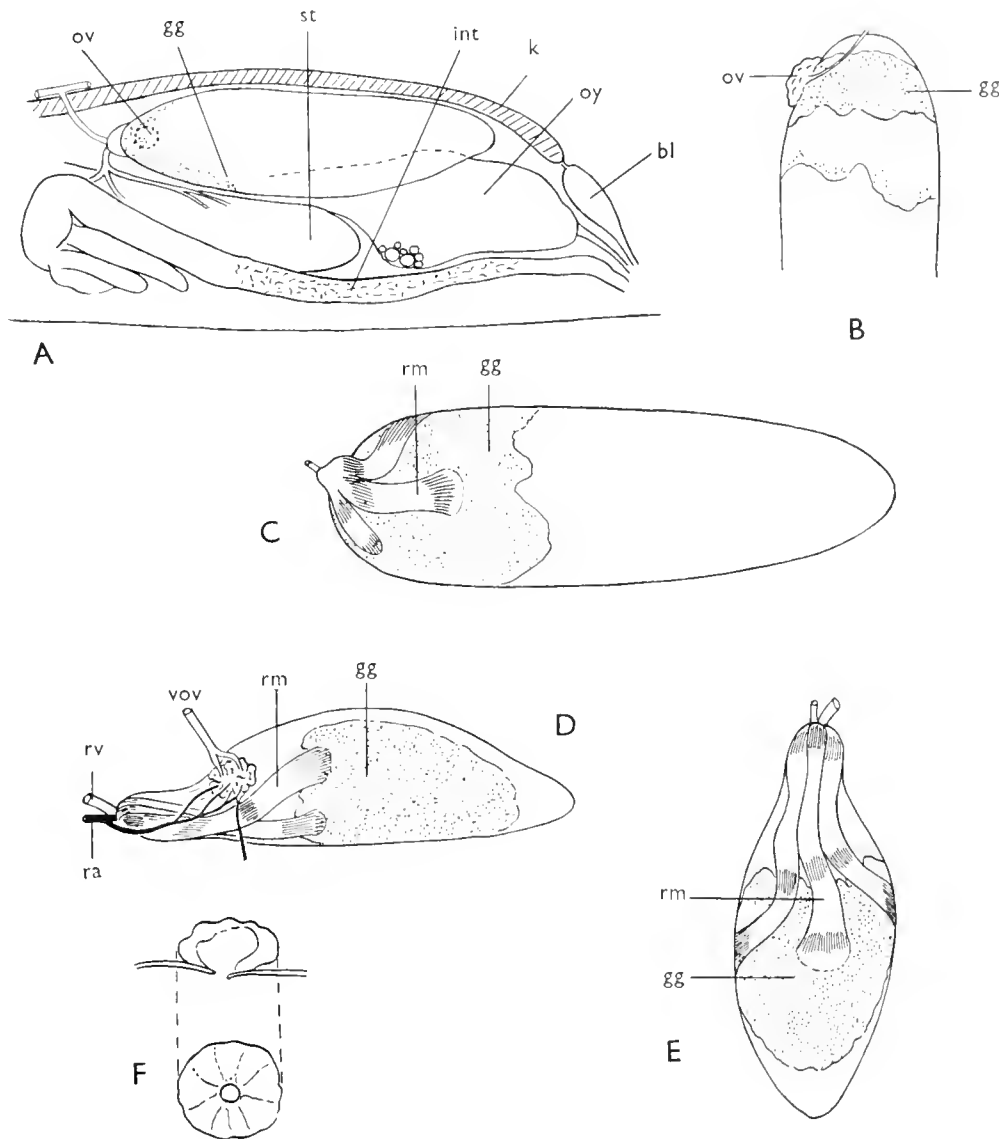
Text-fig. 18. Swimbladders of *Benthosema suborbitale* (A, B, C), and *B. glaciale* (D–F). A, C, D, E, lateral views; B, dorsal view. The almost closed oval of *B. glaciale* is seen in diagrammatic transverse section and from below in (F). *bl*, urinary bladder; *gg*, gas-gland; *int*, intestine; *k*, kidney; *ov*, oval; *oy*, ovary; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *st*, stomach; *vov*, vein to oval. (A, × 11·5; B, × 15; C, × 15; D, × 11; E, × 10; F, × 20.)

Benthosema suborbitale (Gilbert) (Text-fig. 18A–C)

St. 2067, 24° 12′ N., 21° 12·2′ W., 12. v. 37, N 450 H, 68(–0) m. B.M. Reg. no. 1948.5.14. 185–91. Standard length of fish 24 mm. (4·3 × 1·3 mm.).

A thin-walled swimbladder originates over the forepart of the stomach and extends over some two-thirds of the length of the body-cavity.

The gas-gland invests the floor of the foremost third of the organ. As in all myctophids, the gland receives three retia mirabilia, which enter the anterior and lower part of the swimbladder.

Not far behind the forward tip and on the right-hand side of the bladder, the oval, which is almost closed, appears as a small circular blister, about 0·3 mm. in diameter. This has a small opening into the main cavity and the much folded walls have a rich supply of blood capillaries.

Diogenichthys atlanticus (Tåning)

St. 288, 00° 56′ 00″ S., 14° 08′ 30″ W., 21. viii. 27, TYF, 250(–0) m. B.M. Reg. no. 1930.1.12. 846–7. Standard length 25·5 mm. (3·0 × 0·6 mm.).

The swimbladder of this specimen was in a relaxed state, the walls appearing thicker than they would be when the sac is inflated. The three retia mirabilia are bound together in a bulbous forward extension and are closely followed by the gas-gland, which covers about three quarters of the swim-bladder floor.

Myctophum humboldti (Risso)

St 1566, 40° 42′ S, 36° 05·5′ E., 9. iv. 35, N 70 H, 0–5 m. Standard length 50 mm. (8·0 × 4·0 mm.).

This species has a capacious thin-walled swimbladder. The three retia mirabilia run underneath the forward, rounded end of the swimbladder to the gas-gland, which is three lobed and extends over the floor and lateral walls. Each rete is about 3 mm. in length, while the gas-gland has a length of about 2·5 mm. and a width (when flattened out) of about 4·5 mm.

Myctophum affine (Lütken) (Text-fig. 19)

St. 694, 04° 05½′ N., 30° 00′ W., 10. v. 31, NH, 0 m. B.M. Reg. no. 1948.5.14. 234–6. Standard length 51 mm. (9·0 × 4·0 mm.).
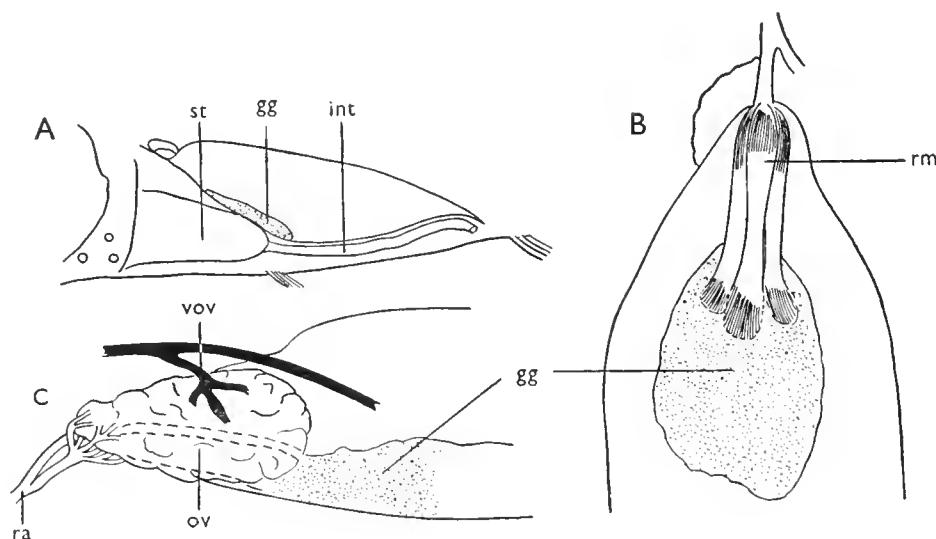
Text-fig. 19. Swimbladder of *Myctophum affine*, seen (A) in body-cavity, (B) ventrally (anterior end), and (C) laterally (anterior end). *gg*, gas-gland; *int*, intestine; *ov*, oval; *ra*, retial artery; *rm*, rete mirabile; *st*, stomach; *vov*, vein to oval. (A, × 4·5; B, × 25; C, × 25.)

The swimbladder is thin walled and extends down some three-quarters of the length of the body-cavity. The retia mirabilia extend back from the foremost tip of the sac and run to an oval-shaped gas-gland lying on the floor of the anterior half. The gland measured 1·5 mm. in length and 1·25 mm. in width, while the retia spanned about 1·5 mm.

To the left of the forward end of the swimbladder is the oval, which is closed, and appears as a wrinkled projection with thick, expanded walls.

Diaphus dofleini Zugmayer (Text-fig. 20 A, B)

St. 250, 36° 09′ 00″ S., 5° 33′ 00″ W., **17**. vi. 27, TYF, 300(–0) m. B.M. Reg. no. 1930.1.12. 831–2. Standard length 32 mm. (6·5 × 1·5 mm.).

This lantern fish has a thin-walled swimbladder, which originates over the forepart of the stomach and spans nearly two-thirds the length of the body-cavity. The retia mirabilia arise to the right of the lower surface of the sac, about 1 mm. behind its forward end. Each rete is nearly 1·5 mm. in length. The three lobes of the gas-gland, which invest the middle part of the swimbladder floor, are roughly oval in outline and measure 2·5 and 1 mm. in length and breadth.
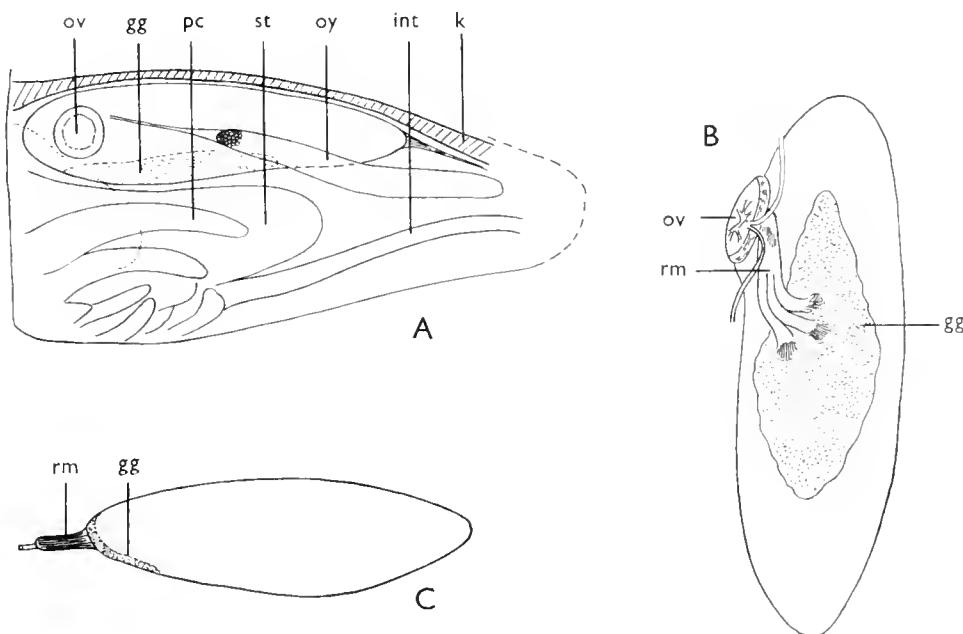
Text-fig. 20. Swimbladders of *Diaphus dofleini* (A and B) and *D. garmani* (C). A and C are lateral views; B is a ventral view. *gg*, gas-gland; *int*, intestine; *k*, kidney; *ov*, oval; *oy*, ovary; *pc*, pyloric caecum; *rm*, rete mirabile; *st*, stomach. (A, × 8; B, × 10; C, × 8·5.)

Just above the point of origin of the retia and on the right side of the sac, the oval appears as a circular cap (about 0·75 mm. in diameter). It is partly open, the capillary-bearing part being surrounded by a ring of connective tissue containing circular and radial muscle fibres.

Diaphus garmani Gilbert (Text-fig. 20 C)

B.M. Reg. no. 1934.5.4. 1–2. Montserrat. Standard length 34·5 mm. (6·0 × 2·0 mm.).

A thin-walled swimbladder was found just above the stomach. The three retia mirabilia are bound together in a club-shaped forward extension of the swimbladder. They are about 1 mm. in length and supply a rather small gas-gland. This extends over the floor and lateral walls of the foremost quarter of the organ.

Diaphus luetkeni (Brauer)

St. 288, 00° 56′ 00″ S., 14° 08′ 30″ W., **21**. viii. 27, TYF, 250(–0) m. B.M. Reg. no. 1930.1.12. 846–7. Standard length 34 mm. (3·5 × 1·2 mm.).

As the swimbladder of this fish was relaxed, the walls appear thick, while the gas-gland occupies most of the floor. When the sac is expanded, the dimensions must be considerably more than those given above.

Standard length 54 mm.

Diaphus agassizii Gilbert

This individual contained a well-developed swimbladder measuring about 7 mm. in length.

Notolychnus valdiviae (Brauer) (Text-fig. 21 D)

St. 1586, 02° 39·4′ N., 50° 46·4′ E., 2. v. 35, TYFB 1650–950(–0) m. B.M. Reg. no. 1948.5.14. 310–25. Standard length 19 mm. (1·5 × 0·75 mm.).

As in other myctophids, the swimbladder originates over the stomach, but is so small that it does not extend beyond this organ. Except for the roof, the gas-gland covers the entire inner surface of the sac. The three retia mirabilia, which have a length of about 1·75 mm., run backwards and upwards along the right lateral wall of the stomach and enter the anterior part of the swimbladder floor.

In another fish (standard length 19·5 mm.) from St. 1586 the swimbladder had a length of nearly 2·5 mm. Though the sac of both fishes was somewhat relaxed, it would seem that the swimbladder of this species is reduced in size.

Lampadena chavesi Collett (Text-fig. 21 A–C)

Position, 51° 23′ N., 11° 47′ W. B.M. Reg. no. 1911.2.8. 1. Standard length 75 mm. (9·5 × 3·5 mm.).

The swimbladder of this lantern fish arises above the forepart of the stomach and extends down the remainder of the body-cavity. The three retia mirabilia enter the right anterior part of the sac and run backwards to supply a gas-gland covering the forward half of the swimbladder floor.

Each rete has an individual length. The innermost one, with a span of about 2·5 mm. supplies the foremost lobe of the gas-gland, while the next lobe is fed by the middle complex, which is 4·5 mm. in extent. The outermost rete is the largest (about 5·75 mm.) and runs to the posterior lobe of the gland.

Alongside the retia, forming an anterior extension of the swimbladder, is a conical projection (presumably the oval) that is well supplied with blood-vessels.

Lampanyctus güntheri Goode & Bean (Text-fig. 22 A)

St. 710, 21° 45′ S., 39° 50′ W., 26. x. 31, TYFB, 294(–0) m. B.M. Reg. no. 1948.5.14. 534–56. Standard length 53 mm. (9·5 × 2·5 mm.).

In this species the swimbladder is a thin-walled sac occupying about four-fifths the span of the body-cavity. The rounded forward extremity lies just behind a vertical line drawn through the base of the pectoral fins.

The three retia mirabilia lie under the forepart of the swimbladder and extend backward to the medially situated gas-gland. Each rete is almost 3 mm. in length, while the gas-gland, which invests the floor and side walls, has a length of 2·3 mm. The artery and vein supplying the retia mirabilia come from the dorsal aorta and hepatic portal system respectively.

Centred above the middle point of the retia and on the left side of the swimbladder, the oval appears as a thin-walled blister, 1·8 mm. in width. This opens into the main cavity through an oval aperture situated in the side wall just above the retia. The walls of the oval are richly supplied with capillaries and larger vessels.

Lampanyctus alatus Goode & Bean (Text-fig. 22 B)

St. 2057, 12° 09′ S., 04° 28·2′ W., 29. iv. 37, N 450 B, 1450–700(–0) m. B.M. Reg. no. 1948.5.14. Standard length 57·0 mm. (9·0 × 2·5 mm.).

This species has a capacious swimbladder extending down about two-thirds the length of the body-cavity. The walls are rather thin but well strengthened, with collagen fibres.

In side view the swimbladder has a gradually tapering forward section, the floor of which is
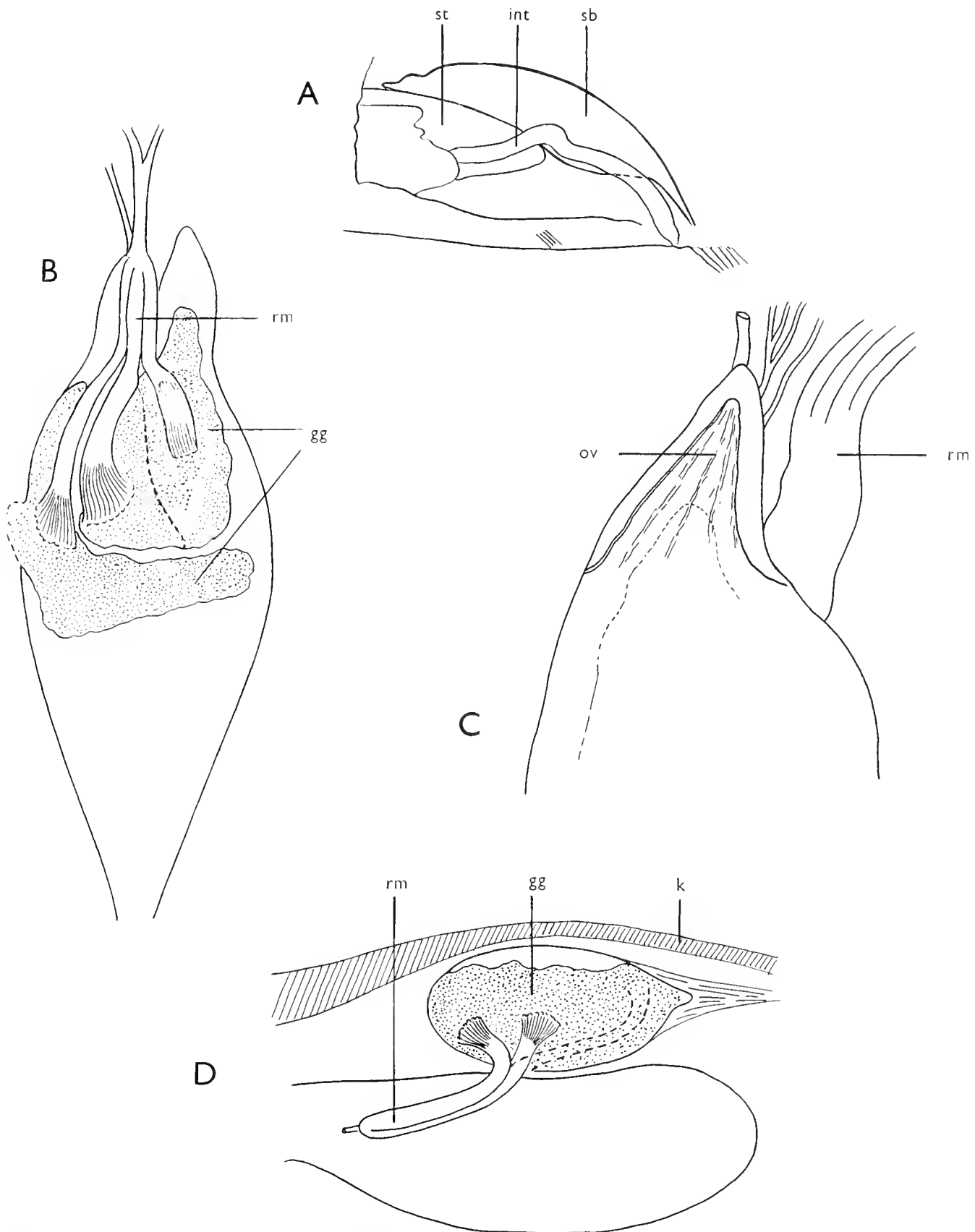
Text-fig. 21. Swimbladders of *Lampadena chavesi* (A) in body-cavity; (B) ventral view; (C) dorsal view (anterior end), and (D) *Notolychnus valdiviae*, lateral view. *gg*, gas-gland; *int*, intestine; *k*, kidney; *ov*, oval; *rm*, rete mirabile; *sb*, swimbladder; *st*, stomach. (A, × 6·9; B, × 9·9; C, × 18·9; D, × 30.)

covered by the gas-gland. This has three lobes, each receiving a rete mirabile. The retia originate in front of the sac, and are bound together to form a cylindrical structure, before diverging over the under surface of the gas-gland. The left, middle and right retia have lengths of about 2·5, 3·0 and 4·0 mm. respectively, differences parallel to those found in *Lampadena chavesi*.
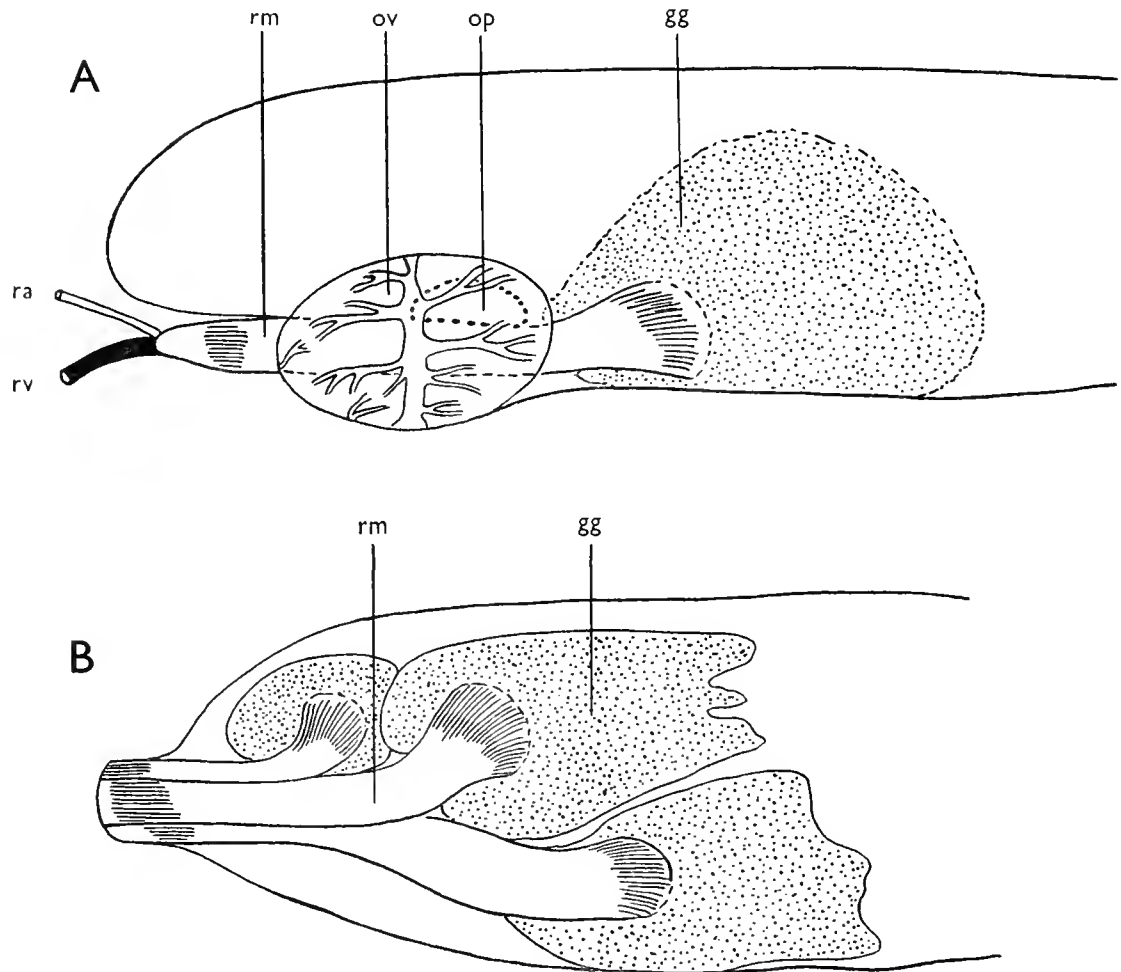
Text-fig. 22. Swimbladders of *Lampanyctus guentheri* (A) lateral view of anterior half, and *L. alatus* (B), ventral view of anterior half. *gg*, gas-gland; *op*, opening of oval into main cavity of swimbladder; *ov*, oval; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (A, × 27; B, × 22·5.)

Lampanyctus pusillus (Johnson)

St. 1602, 17° 59·9′ S., 04° 27·1′ E., 27. x. 35, TYFB, 175(–0) m. B.M. Reg. no. 1948.5.14. 389–91. Standard length 22 mm. (3·0 × 0·5 mm.).

St. 100 C, 33° 20′–33° 46′ S., 15° 18′ –15° 08′ E. 4. x. 26, TYF, 2500–2000(–0) m. B.M. Reg. no. 1930.1.12. 762–3. Standard length 33 mm. (6·5 × 1·5 mm.).

The swimbladder of this species lies over the posterior half of the stomach and extends beyond it as far as the level of insertion of the pelvic fins. In both specimens the sac is considerably relaxed.

The retia mirabilia originate to the left of the anterior tip of the swimbladder and extend backwards to the gas-gland, which covers the forward part of the floor. Close examination of the 33-mm. fish revealed that each rete has a different length. The inner one supplies an anterior lobe of the gas-gland, the middle one a middle lobe and the outer one a posterior lobe. Their lengths in the order given are 3·0, 2·3 and 1·8 mm.

An oval is present on the roof of the sac above the forward part of the retia.

Gymnoscopelus nicholsi (Gilbert) (Text-fig. 23)

St. WS 213, 49° 22' S., 60° 10' W., 30 v. 28, N 4–T, 249–259 m. B.M. Reg. no. 1948.5.14. 621–6. Standard length 50 mm.

The swimbladder, which is found over the middle region of the stomach, measured no more than 2·5 mm. in length. As in all myctophids, three retia mirabilia, which are closely bound together, enter the anterior end of the swimbladder. The gas-gland is oval in outline and invests the floor of the swimbladder over its anterior half. The walls of the bladder are so thick that little remains of the inner cavity. Clearly, the organ has undergone considerable regression.
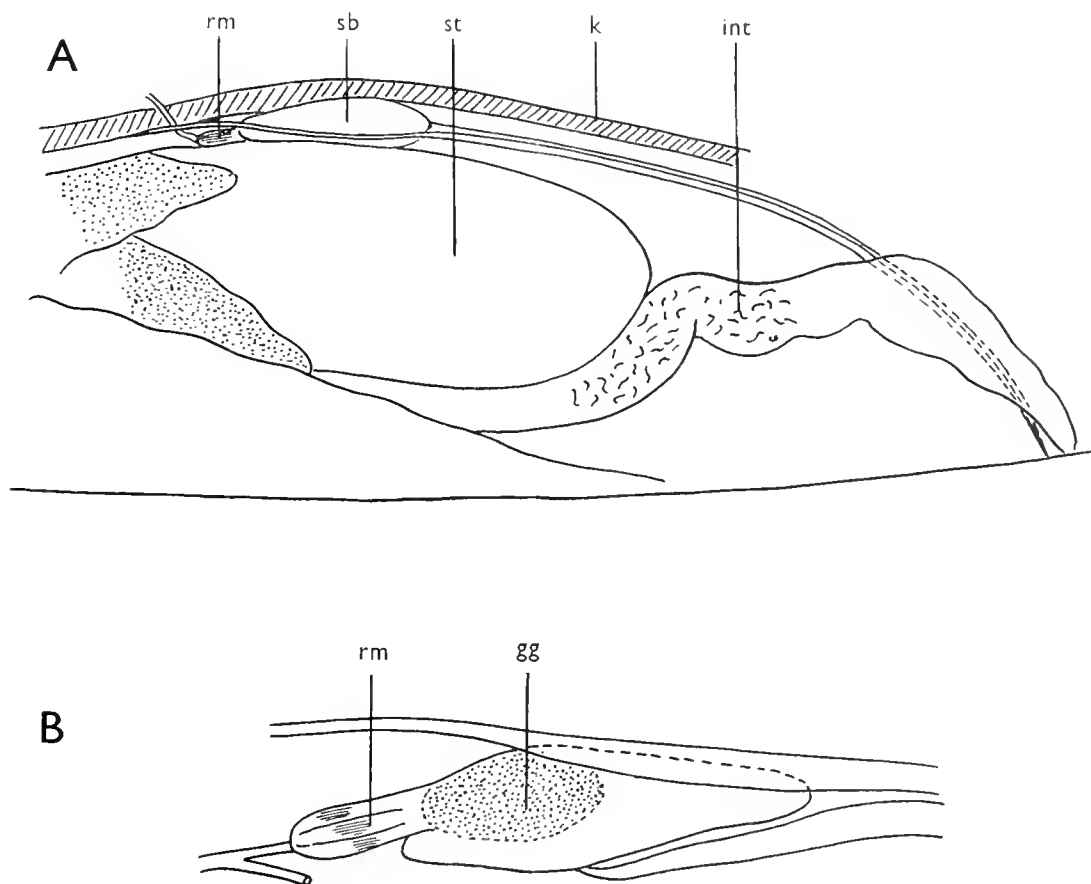
Text-fig. 23. Swimbladder of *Gymnoscopelus nicholsi* (A) seen in position in body-cavity, and (B) ventral view. *gg*, gas-gland; *int*, intestine; *k*, kidney; *rm*, rete mirabile; *sb*, swimbladder; *st*, stomach. (A, × 12; B, × 22·5).

Ceratoscopelus townsendi (Eigenmann & Eigenmann)

St. 703, 10° 59·3' N., 27° 03·8' W., 17. x. 31, TYFB, 358–0 m. B.M. Reg. no. 1948.5.14. 584–5. Standard length 55·0 mm. (5·5 × 1·5 mm.).

Being in a rather relaxed condition, the swimbladder of this fish did not extend beyond the pyloric end of the stomach. The three retia mirabilia enter the floor of the sac at its forward end to supply a gas-gland that extends from one extremity to the other. However, when the sac is expanded conditions may well be different.

Opposite the point of entry of the retia is the oval, which has the appearance of a collapsed blister. The capillary network is fed through a vessel from the retial artery, while the return circulation is by way of a large vein running upwards to the roof of the body-cavity.

No trace of a swimbladder was found in adults of the following species: *Gonichthys coccoi* (Cocco), *Ctenobranchus nigro-ocellatus* (Günther), *Diaphus coeruleus* Klunzinger, and *Gymnoscopelus braueri* (Lönnberg).

Family Neoscopelidae

Neoscopelus macrolepidotus Johnson (Text-fig. 24)

John Murray Expedition St. 145, Maldive Area, 494 m. B.M. Reg. no. 1939.5.24. 475–84. Standard length 118 mm. (30·0 × 10·0 mm.).

A capacious swimbladder with rounded anterior and tapering posterior extremities runs down the greater part of the upper body-cavity. The lower half of the sac, which is rather thick walled, is invested with pigmented peritoneum.
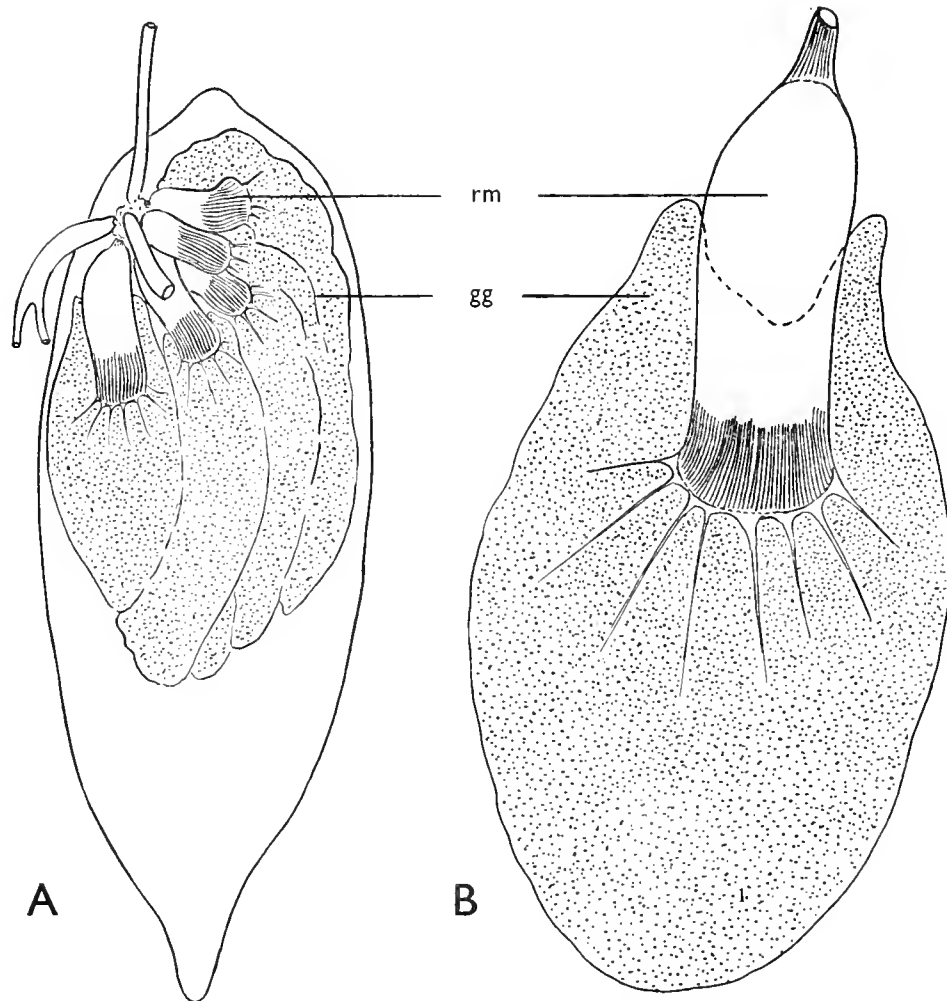
Text-fig. 24. Swimbladder of *Neoscopelus macrolepidotus*, seen (A) from below. In (B) is shown a single rete and lobe of the gas-gland. *gg*, gas-gland; *rm*, rete mirabile. (A, × 3·9; B, × 9·3.)

The gas-gland covers some two-thirds of the floor of the sac and is fed by five massive retia mirabilia. These originate from a blood-vessel junction, which is found on the right-hand side of the anterior under-surface of the swimbladder. The junction receives a large vein from the hepatic portal system and an artery from the system of vessels on the roof of the stomach. There is also a blood-vessel (probably an artery) running backwards to the junction from the forward end of the swimbladder. But the fish is so poorly preserved that it is impossible to trace the blood-system with any certainty.

A careful search was made for the resorptive part of the swimbladder. No trace of an oval could be seen or indeed of any such special capillary bearing region.

Scopelengys tristis Alcock

I have confirmed Alcock's (1899) finding that this species has no swimbladder.

Family SCOPELOSAURIDAE

In this family, which consists of several species belonging to a single genus, the swimbladder is absent in adolescent and adult individuals. The larvae have not been examined.

Suborder ALEPISAUROIDEA

Elsewhere I have stated that these iniomous fishes have no swimbladder (Marshall, 1955).

Order *MIRIPINNATI*

The swimbladders of these oceanic fishes have already been described (Bertelsen and Marshall, 1956). During the larval phase the swimbladder is functional, but it regresses during the adolescent phase and in *Mirapinna*, at least, is a rudimentary structure in the adult.

. There are two retia mirabilia receiving blood-vessels that extend forwards from the posterior end of the swimbladder. In a larval *Parataeniophorus gulosus* of standard length 27·5 mm. the front part of the sac is thick-walled and the walls are invested with a well-developed gas-gland on either side. The posterior part of the sac is thin-walled and is presumably concerned in the resorption of gases.

In an adolescent *P. festivus* of standard length 42·0 mm. the thin-walled part of the swimbladder is much reduced and the retia mirabilia and gas-gland have begun to regress. In the rudimentary organ of *Mirapinna*, these structures are barely recognizable.

Order *CETUNCULI*

Family CETOMIMIDAE

Ditropichthys storeri (Goode & Bean)

St. 2059, 09° 11·4' S., 05° 17·4' W., 30. iv. 37, N 450 B, 1900–1400 m. Standard length 30 mm.

In this fish a small swimbladder was found with a strong attachment to the roof of the stomach. The sac measured about 2·5 mm. in length. Entering the posterior end of the sac was an artery coming from a vessel running along the stomach wall. Another vessel originating in the roof of the body-cavity ran to the 'anterior' end.

Transverse sections through this organ revealed it to be much regressed, the small lumen having a curiously complicated form. Much of the bulk of the swimbladder is formed by a voluminous submucosa. The sections suggest that during the regression of the organ, the sac becomes doubled back, the anterior and posterior ends coming together at the back. Within the lumen there were remnants of the cells composing the gas-gland.

The interpretation of this curiously regressed organ must be left until earlier stages in the life-history become available. Evidently the larvae of this species have a well-formed gas-filled swimbladder.

Cetostoma regani (Zugmayer)

No trace of a swimbladder was found in this species.

Family RONDELETIIDAE

Rondeletia bicolor Goode & Bean

Parr (1929) records the absence of the swimbladder in this species.

Order *GIGANTUROIDEA*

Regan (1925) included the absence of a swimbladder in his diagnosis of this order. I was unable to find any trace of this organ in a *Gigantura vorax* of standard length 74 mm.

Order *LYOMERI*

Bertin (1934) has given an account of the internal organs of *Eurypharynx pelecanoides* and *Saccopharynx ampullaceus*, but no mention is made of a swimbladder. I was unable to find this organ in an individual of the first species.
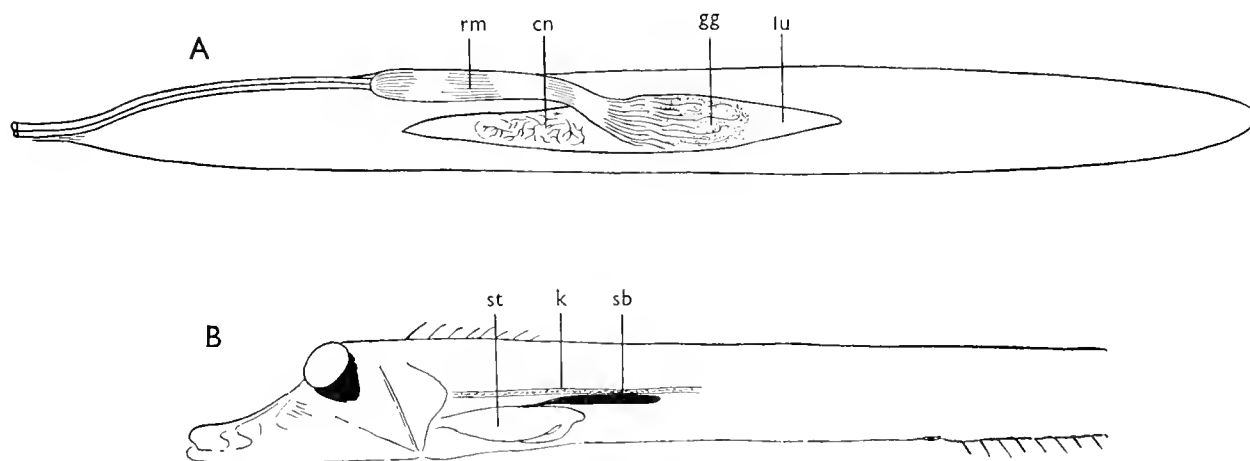
Text-fig. 25. Swimbladder of *Stylophorus chordatus*, seen (A) from below, and (B) in the body-cavity of the fish. *cn*, capillary network; *gg*, gas-gland; *k*, kidney; *lu*, lumen of swimbladder; *rm*, rete mirabile; *sb*, swimbladder; *st*, stomach. (A, × 15; B, × 1·8.)

Order *ALLOTRIOGNATHI*

Family STYLOPHORIDAE

Stylophorus chordatus Shaw (Text-fig. 25)

St. 296, 8° 12′ N., 18° 49′ W., 26. viii. 27, TYF, 450–500(–0) m. Standard length 177 mm.

This individual contained a small elongated swimbladder, lying just below the black-speckled kidneys and originating a little before the pyloric end of the stomach. The sac measured about 12·5 mm. in length and 1·0 mm. in diameter and is attached by a mesentery to the dorsal wall of the stomach.

Within the mesentery is an artery and vein running close together to the anterior end of the sac. The two vessels continue together for about 3 mm. along the left-hand lateral walls and then subdivide to form a single rete mirabile having a length of about 2 mm. The rete enters the lumen of the sac about half-way along its length (of about 4 mm.).

Examination of serial transverse sections revealed the disposition of the resorbent and glandular parts of the swimbladder. The capillaries of the former lie just below the inner epitheleum and occur over much of the lumen anterior to the point of entry of the rete. The glandular tissue lies behind this point in the posterior half of the lumen. In supplying the gland, the retial capillaries do not unite to form larger vessels. The rete is thus unipolar.

Reference to Text-fig. 25 will show the small volume of the lumen compared with the total volume of the sac. Between the inner epithelium and the tunica externa is a voluminous layer of lamellar fibres belonging to the submucosa, which thus makes up most of the total volume. Clearly this is a regressed swimbladder, which is doubtless relatively better developed during the early life-history.

In having a swimbladder with clearly separate glandular and resorbent parts, *Stylophorus* is evidently an euphysoclist. But it is unusual in having these two parts reversed in position, for in most euphysoclists (without an oval) the fore part is secretory, while the rear part is resorbent.
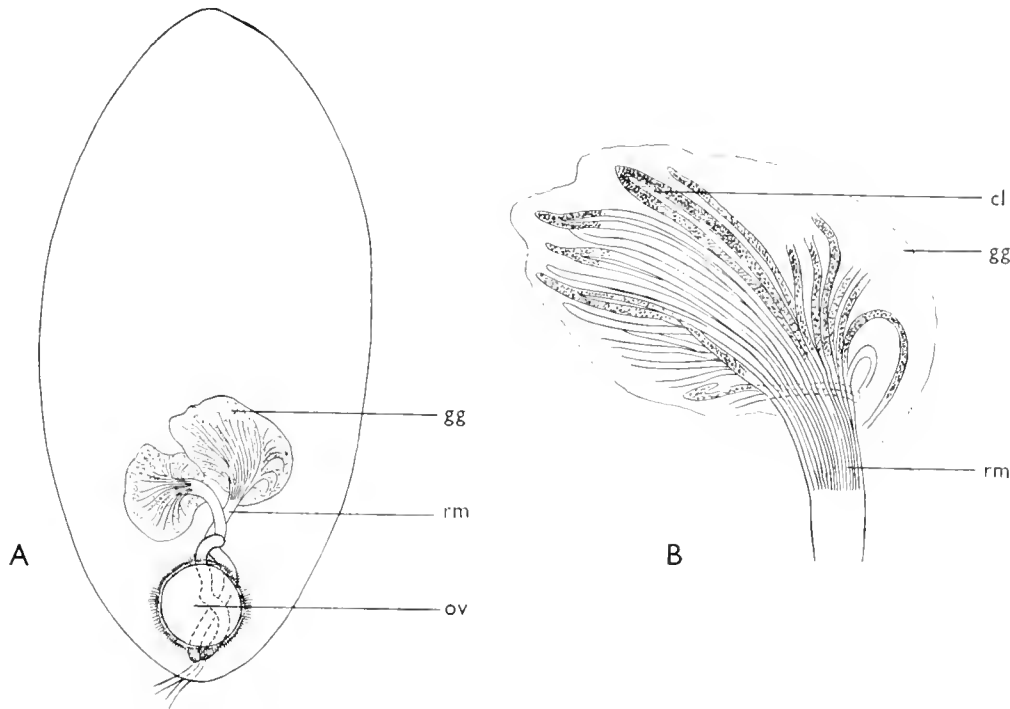
Text-fig. 26. Swimbladder of *Stephanoberyx monae*, seen (A) from above. In (B) is shown the blood supply to the right lobe of the gas-gland. *cl*, capillary loop; *gg*, gas-gland; *ov*, oval; *rm*, rete mirabile. (A, × 5·5; B, × 17.)

Order BERYCOMORPHI

Family STEPHANOBERYCIDAE

Stephanoberyx monae Gill (Text-fig. 26)

Oregon St. 1426 (29° 07′ N., 87° 54′ W.), 24. ix. 57, 600 fathoms, trawl. Standard length 83·5 mm. (16·0 × 8·0 mm.).

The swimbladder of this species is ellipsoidal in form and extends down most of the length of the upper part of the body-cavity.

The blood supply for the retia enters the floor of the sac close to its posterior end. The artery and vein form two long retia mirabilia (about 8 mm. in length). In the fish dissected the retia were displaced in position, but presumably extend forward along the swimbladder floor. Each rete runs to a corresponding lobe of the gas-gland, where the capillaries form loops running through the secretory tissue. The retia are thus unipolar in structure.

Immediately above this point of entry of the retial blood supply there is an oval on the roof of the sac. This measured about 5 mm. in diameter and was partly closed. The capillary network of this resorbent structure was plainly visible under the high power of a binocular microscope.

Family Melamphaidae

Melamphaes megalops Lütken (Text-fig. 27)

St. 13° 25′ N., 18° 22′ W., 28. x. 25, 4½-m. net, horizontal 900(–0) m. Standard length 56 mm. (8·5 × 5·0 mm.).

In this species there is a capacious swimbladder which, when fully inflated, must occupy about three-quarters of the length of the upper part of the body-cavity.
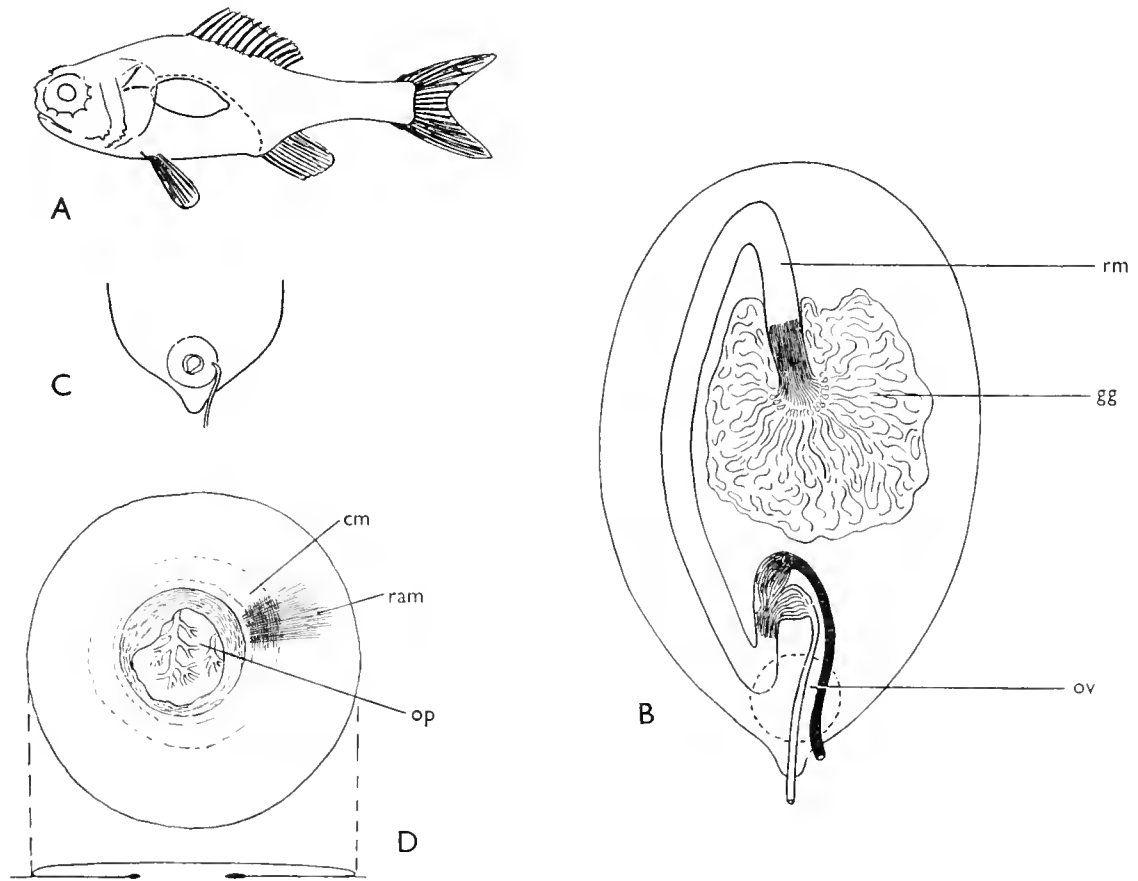
Text-fig. 27. Swimbladder of *Melamphaes megalops*, seen (A) in fish; (B) ventrally, and (C) dorsally (posterior end). The oval is shown in (D). *cm*, circular muscles of oval; *gg*, gas-gland; *op*, opening of oval into cavity of swimbladder; *ov*, oval; *ram*, radial muscles of oval; *rm*, rete mirabile. (A, × 1; B, × 10; C, × 5; D, × 25.)

At the posterior end of the sac, an artery and vein run forward to supply a single rete mirabile, which measures about 12 mm. in length. After its formation the rete runs backwards but soon bends sharply to run along the right-hand side of the gas-gland. Having reached a point ahead of the forward edge of the gas-gland, it turns back to enter the gland. Here it separates into capillary loops that meander among the secretory cells. As in *Stephanoberyx*, the rete is unipolar. An extensive gas-gland covers the median part of the swimbladder floor, the length and breadth being about 3 mm.

Just in front of the posterior tip and on the roof of the sac is an oval (about 2 mm. in diameter), which was almost closed, the entry into the sac measuring about 0·5 mm. in width.

The circular sphincter muscles that close the oval could be seen around the rim of the opening, where they are crossed by the long relaxed fibres of the radial complex. When these contract, the oval is expanded, the capillary network then being fully exposed to the gases in the swimbladder. During this phase gases are free to diffuse into the blood.

Melamphaes unicornis Gilbert (Text-fig. 28 E, F)

St. 3484, 39° 55′ N., 20° 01′ W., 1. x. 56, IKMT, 750(–0) m. (estimated). Standard length 51 mm. (6·5 × 2·5 mm.).

The swimbladder of this melamphaid, which was quite relaxed, lies above the posterior half of the stomach.

Blood-vessels running down from the roof of the body-cavity enter the swimbladder roof at the posterior end, where they supply the oval, which was completely closed.

The single rete mirabile is about 3 mm. in total length. Since the sac is much contracted the rete may well have been displaced forward from its natural position. In this swimbladder it originates in a median lateral position and runs forward and across the floor of the sac, then turning backward to the gas-gland, which is indented along its posterior edge.

Melamphaes mizolepis (Günther) (Text-fig. 28 B–D)

St. 288, 00° 56′ S., 14° 08·5′ W., 21. viii. 27, YFT, 250(–0) m. B.M. Reg. no. 1930.1.12. 1031–40. Standard lengths of two individuals examined 15 and 37 mm.

In the smaller of the two fishes dissected a small spherical swimbladder was discovered over the anterior part of the stomach. It measured 0·4 mm. in diameter. The rete mirabile runs forward to enter the posterior part of the swimbladder roof and then turns sharply downward to follow the outline of the organ as far as the front part, where it joins the gas-gland. This is a compact spherical structure almost filling the lumen.

The posterior tip of the rete appeared to be closely bound to the stomach. Actually two branches from the blood-vessels running over the stomach enter the rete.

The structure of the swimbladder in the larger fish was very similar. The diameter was 0·8 mm. In both individuals it is obvious that the swimbladder is little more than a regressed organ.

Melamphaes cristiceps Gilbert

St. 101, 33° 50′ to 34° 13′ S., 16° 04′ to 15° 49′ E., 15. x. 26, N 450 H, 1310–1410 m. B.M. Reg. no. 1930.1.12. 1006–8. Standard length of fish 80 mm.

A small swimbladder was found behind the stomach and just in front of the ovaries. It measured 3·5 mm. in length. As in *M. mizolepis*, the rete mirabile runs round much of the swimbladder before entering the gas-gland. It is evident that the swimbladder of this species is also regressed.

A fully developed swimbladder is also found in *Melamphaes macrocephalus*, *M. nigrofulvus*, *M. opisthopterus* ? *M. nycterinus* and *M. cristiceps* ? (Kanwisher and Ebeling, 1957).

Family ANOPLOGASTRIDAE

Anoplogaster longidens (Gill) (Text-fig. 28 A)

St. 239, 46° 56′ S., 46° 03′ W., 2. vi. 27, N 450, 1050–1350(–0) m. B.M. Reg. no. 1930.1.12. 974–6. Standard length of fish 98 mm.

In the medium-sized individual examined the swimbladder was found to be a small, almost spherical sac overlying the foremost part of the stomach. Excluding the retia mirabilia, it measured rather more than 3 mm. in length and about 2 mm. in greatest depth. The walls are thick and tough.

Two retia mirabilia about 1 mm. in length enter the posterior end of the swimbladder, each running to a lobe of the gas-gland. Together the two glandular lobes invest the floor and lateral walls of the sac.

The swimbladder is surrounded by fatty tissue which is continued backwards for about 20 mm. to taper off above the end of the stomach. The blood supply for the retia mirabilia came from vessels within the fat body.
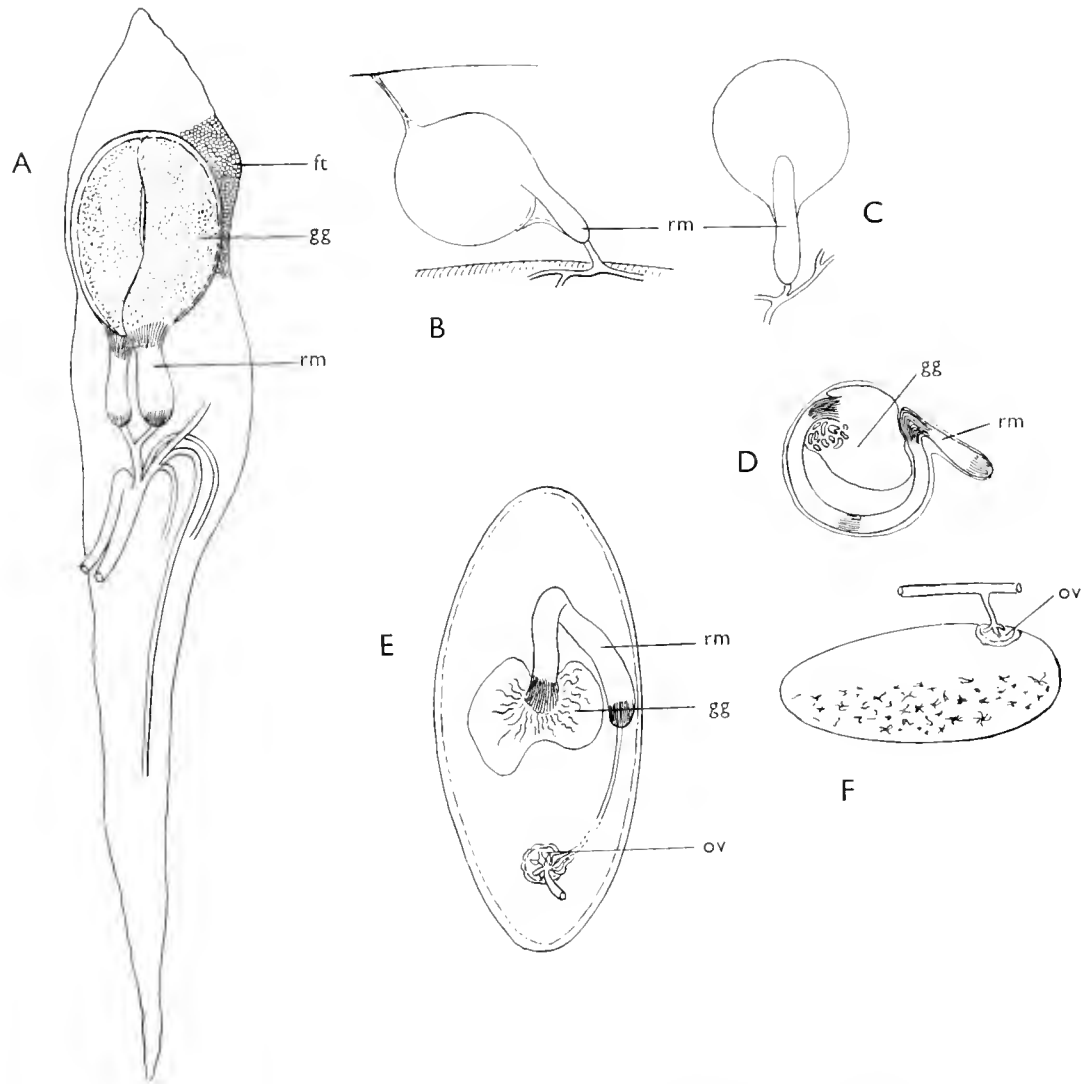
Text-fig. 28. Swimbladders of *Anoplogaster longidens* (A) seen from below; *Melamphaes mizolepis*, (B) lateral view, (C) dorsal view, (D) lateral view; *M. unicornis*, (E) dorsal view; (F) lateral view. *ft*, fat investment; *gg*, gas-gland; *ov*, oval; *rm*, rete mirabile. (A, × 8·5; B, C, D, × 25; E, × 10; F, × 6.)

From this dissection it would appear that in adult *Anoplogaster* the swimbladder can have very little hydrostatic function.

Order *PERCOMORPHI*

Family CHIASMODONTIDAE

Chiasmodon niger Johnson (Text-fig. 29)

St. 239, 46° 56′ S., 46° 03′ W., 2. vi. 27, N 450 H, 1050–1350(–o) m. B.M. Reg. no. 1930.1.12. 1058. Standard length 50 mm. (8·0 × 1·5 mm.).

Position, 6° 55′ N., 15° 54′ W., 2-m. tow-net, horizontal, 800(–o) m. B.M. Reg. no. 1930.1.12. 1057. Standard length 49 mm. (8·0 × 1·5 mm.). B.M. Reg. no. 1922.5.26. 1–2. Madeira. Standard length 104 mm. (21·0 × 3·0 mm.).

In each of the three fishes examined, the swimbladder is an elongated ellipsoidal sac, which in the 104 mm. specimen occupied the greater part of the upper half of the body-cavity.

The retia are formed from an artery and vein that enter the forward tip of the sac. In the 49-mm. fish there were eight, each running backward to supply a corresponding lobe of the gas-gland and having a length of 3·25 mm. A closely similar retial measurement was also obtained from the largest individual.

In the 50-mm. fish a transverse diaphragm was found in the posterior half of the swimbladder. There is an aperture in the central part of the diaphragm, through which the anterior chamber containing the retia and gas-gland, communicates with the posterior chamber. It is clear that the structure of the swimbladder of *Chiasmodon* is essentially similar to that found in other physoclist teleosts, in which a diaphragm separates an anterior gas-producing chamber from a posterior resorbent
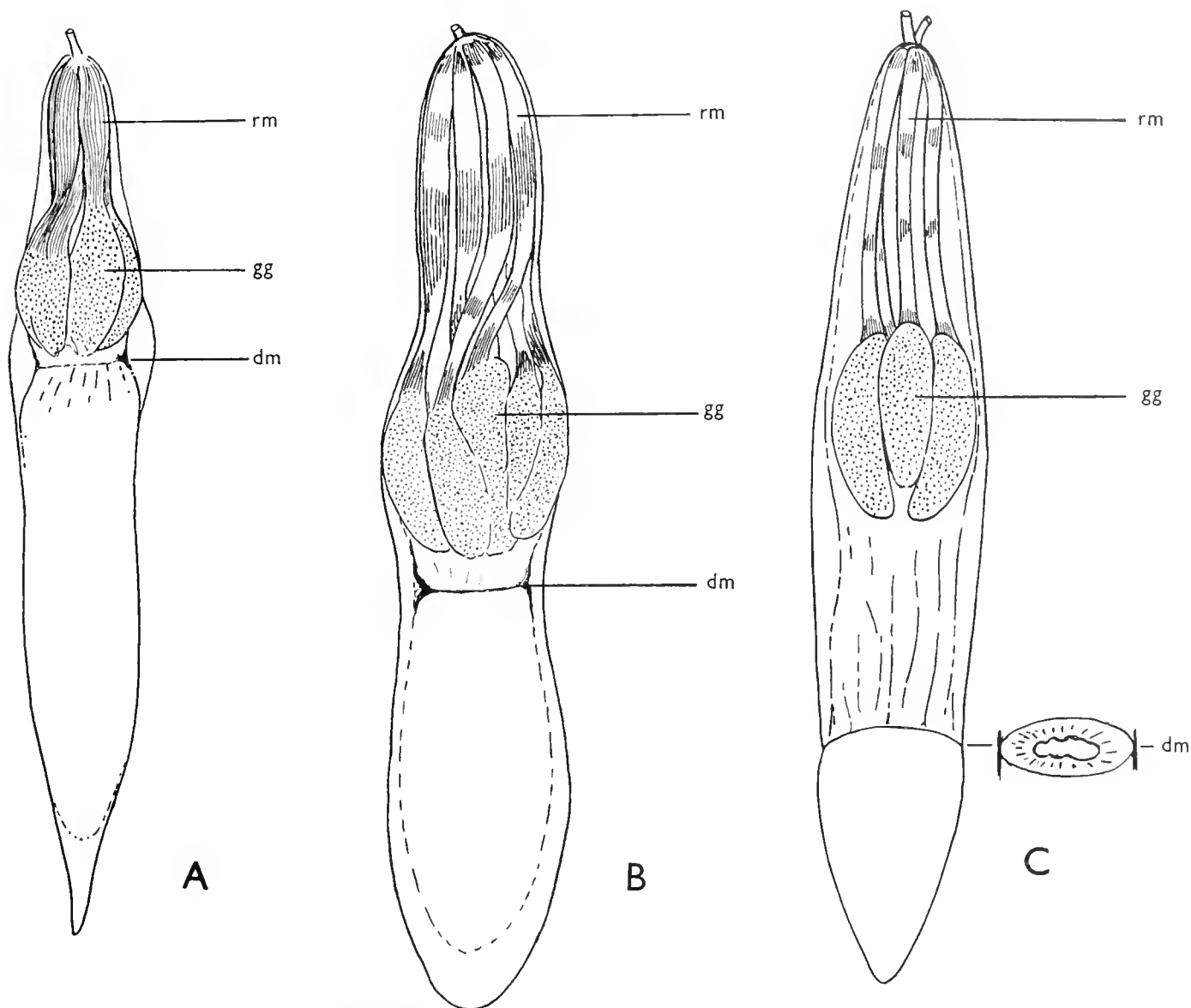
Text-fig. 29. Swimbladder of *Chiasmodon niger* (ventral view), seen in three different states of activity; (A) with the resorbent posterior chamber well expanded, (B) with the gas-secreting and resorbent chambers about equal in volume, and (C) with the gas-secreting chamber well expanded. *dm*, diaphragm; *gg*, gas-gland; *rm*, rete mirabile. (A, × 6·9; B, × 19·5; C, × 18.)

chamber. It is also evident that the relative volumes of these two chambers vary in the three specimens. In the largest fish the diaphragm is close behind the gas-gland in the anterior third of the swimbladder, while it occupies a median position in the 49-mm. individual. These variations will be considered at greater length in the section concerned with gas resorption (p. 81).

The swimbladder is absent in two other members of the Chiasmodontidae, *Pseudoscopelus scriptus* and *Dysalotus alcocki*.

Order *PEDICULATI*

Suborder CERATIOIDEA

The combined researches of Garman (1899), Waterman (1948), R. Clarke (1950) and Bertelsen (1951) show that the deep-sea angler fishes have no swimbladder. Bertelsen's work reveals that this organ is also absent in the larvae.

STRUCTURE AND SYSTEMATICS

The foregoing survey has revealed that the species of major groups of bathypelagic fishes (Stomiatoidea, Salmonoidea, Myctophidae and Anoplogastroidea) have swimbladders conforming to an individual structural pattern or bauplan. Within each group there are, so to say, variations on an original structural theme. The bearing of these findings on classification will now be considered.

Order *Isospondyli*

Deep-sea isospondylous fishes with a swimbladder are all physoclists: they lack a pneumatic duct, which in physostomatous Isospondyli connects the swimbladder to the foregut. The acquisition of a closed swimbladder in these stomiatoids and deep-sea salmonoids must have been imposed on them by their living-space in oceanic mid-waters. The physostomatous isospondyls live in the relatively shallow seas over the continental shelves, or in freshwater. While at least some of these forms can secrete gas, this is a slow process, but they are readily able to inflate their swimbladders by gulping in air at the surface and forcing it down the pneumatic duct. On the other hand, a visit to the surface by a hypothetical physostome living several hundred metres below the surface is clearly 'out of the question'. Such a fish would not only be faced with a long climb to the surface, but having replenished the swimbladder gases, would then have to resolve the problem of the gradient in hydrostatic pressure as it returned to its level in the ocean. After diving to a depth of say, 500 m., the volume of the swimbladder would be compressed to about one-fiftieth of its capacity at the surface. If the fish is to use its swimbladder as a hydrostatic organ, it must then secrete gas, and to make up the volume (to 5 per cent of the body volume, see p. 68) at a pressure of 50 atmospheres would obviously require highly developed retia mirabilia and gas-glands. The retention of a pneumatic duct and air-gulping habits by a mid-water, deep-sea fish is therefore a biological *reductio ad absurdum*.

Suborder Stomiatoidea

The stomiatoid swimbladder has a character complex which may be defined as follows: It is paraphysoclistous[1] with a single, bipolar rete mirabile at the posterior end. As might be expected, the blood supply to the rete comes from vessels originating behind the swimbladder. The capillary network of the resorbent surface arises from a side branch of the retial artery and part of the venous circulation to the gas-gland. The venous blood thus eventually passes through the rete. The gas-producing complex is highly developed, the gland consisting of one to four lobes. A schematic diagram is shown in Text-fig. 30 A.

Comparison of this definition with that of any of the following groups (pp. 53–56) will fully reveal the very characteristic design of the stomiatoid swimbladder. It will also provide further support for the classification of the stomiatoids as a distinct suborder of the Isospondyli.

Regan (1923) was the first to appreciate the essential unity of the stomiatoids. His definition of the

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[1] This term was introduced by Rauther (1922) and refers to simple closed swimbladders in which the glandular and resorbent parts are not sharply localized. It is contrasted with the euphysoclistous type, the resorbent part of which is clearly separate from the glandular part, being either in the form of an oval, or an anterior or posterior section of the sac. In the latter forms, the two parts are often divided by a diaphragm. Fänge (1953) has also pointed out that in euphysoclists the resorbent part is thin-walled, while the glandular part is thick-walled. In paraphysoclists there is no such distinction.
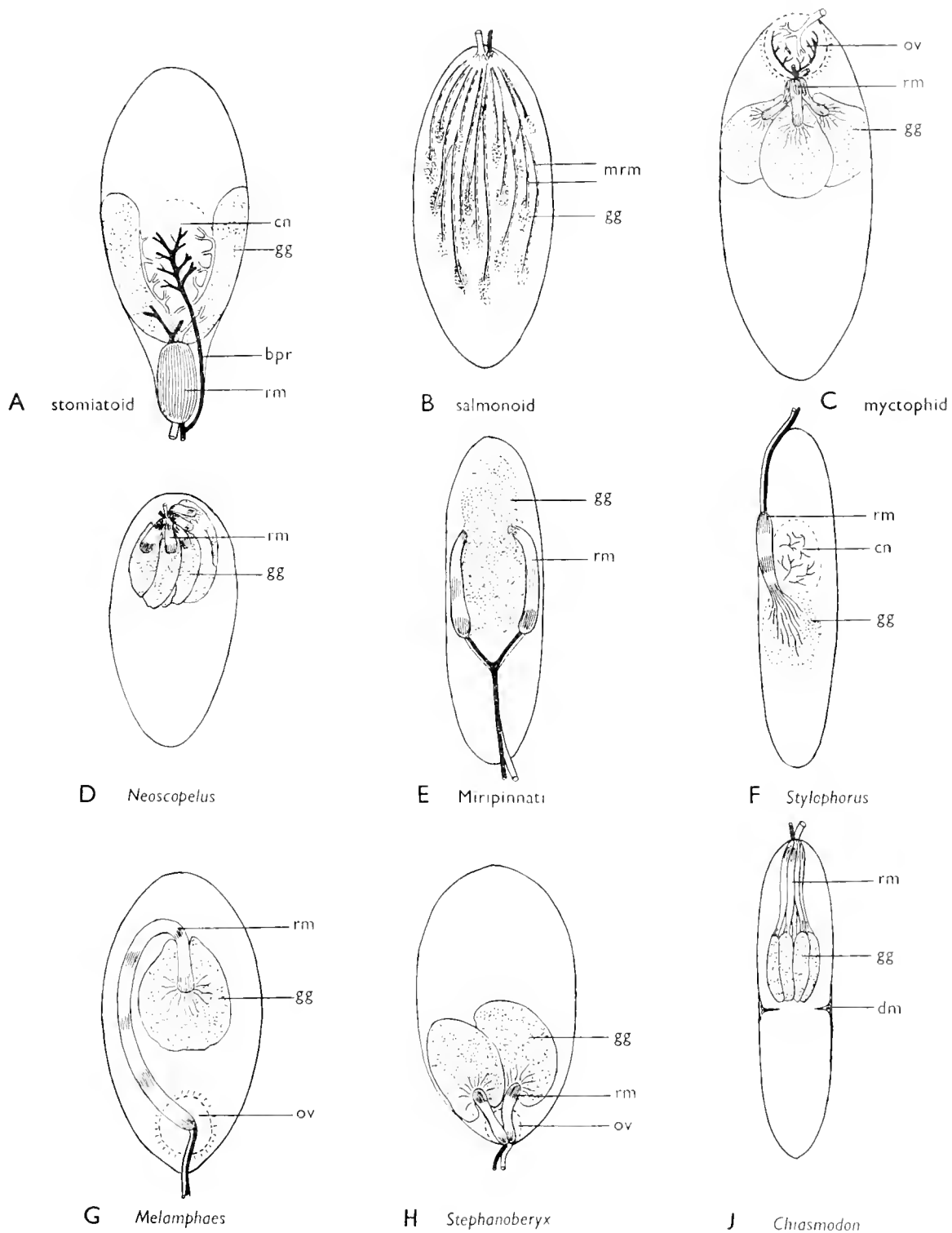
Text-fig. 30. Schematic diagrams showing the essential structural features of the swimbladders of (A) stomiatoids, (B) deep-sea salmonoids, (C) Myctophidae, (D) *Neoscopelus*, (E) Miripinnati, (F) *Stylophorus*, (G) *Melamphaes*, (H) *Stephanoberyx*, (J) *Chiasmodon*. Arteries shown black, veins white. *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *dm*, diaphragm; *gg*, gas-gland; *mrm*, micro-rete mirabile; *ov*, oval, *rm*, rete mirabile.

group was later somewhat amplified (Regan and Trewavas, 1929). The stomiatoids were regarded as being most closely related to the clupeoids, but differing from them in possessing photophores. Certain alepocephalids and searsids, which are clupeoids, also have light organs, but the individual feature of the stomiatoid photophore pattern is the presence of one or two series of lights along each side of the mid-ventral line and one or more photophores associated with each eye (Brauer, 1908; Marshall, 1954).

It is evident that much of Regan's appreciation of the stomiatoids could not be put into words.[1] At all events his definition of them has proved to be inadequate. But when the swimbladder characters are considered together with those Regan used, the stomiatoids are revealed as a 'natural' mono-phyletic group. The implications of this will best be discussed at later stages in this systematic section.

Turning now to the arrangement of the stomiatoids into families, study of the swimbladder provides no new insight. It will be remembered that the Chauliodontidae, Melanostomiatidae, Malacosteidae and Idiacanthidae have no swimbladder, while such features as can be seen in the rudiments of this organ in certain of the Stomiatidae are merely typical of the suborder. Even in the Gonostomatidae, Sternoptychidae and Astronesthidae, which have swimbladders, the knowledge gained has little bearing on their relationships. This may best be shown by the following illustration:

Considering the first two families, Hubbs (1953) has cogently urged that they should again be referred to a single family, Sternoptychidae, with subfamilies Gonostomatinae, Maurolicinae and Sternoptychinae. Hubbs sees these subfamilies (in the order given) as forming a series ranging from forms with generalized to those with specialized body-shapes. Comparison of the swimbladder structure in the three groups also shows that there are no clear-cut differences between them, but if swim-bladder characters alone were considered, the Astronesthidae could also be put with them (and into the same family). However, the other characters of the Astronesthidae indicate that they are best regarded as a separate family and that they are closer to the Chauliodontidae and Melanostomiatidae than to the gonostomatids and sternoptychids (Regan and Trewavas, 1929).

At the generic level, however, swimbladder characters can be of use in definitions, but not always. This may best be shown by short descriptions under the genera that were studied:

Family GONOSTOMATIDAE

Gonostoma. The differences between the swimbladders of *G. denudatum* and *G. elongatum* are so great that no common features can be found to typify the genus.

Cyclothone. The larval swimbladder (in which the gas-gland is found anteriorly), regresses and becomes invested with fat in the adult.

Pollichthys. An oval-shaped resorbent area on the floor of the swimbladder is surrounded by a horseshoe-shaped, single-lobed gas-gland. The bladder is ellipsoidal in form.

Vinciguerria. The resorbent area lies between the rete mirabile and a boomerang-shaped single-lobed gas-gland, which extends over the floor and side walls of the median part of the swimbladder.

Photichthys. The swimbladder of this gonostomatid is readily distinguished from those of other genera by its elongated tubular form.

Maurolicus. The gas-gland consists of two pairs of lobes, a smaller pair near the rete mirabile and a larger pair on the floor of the mid-region of the bladder. The resorbent area lies between these lobes.

Bonapartia. There is a single lobe to the gas-gland, immediately in front of which comes the resorbent area, which invests the floor of the swimbladder.

Ichthyococcus. The gas-gland has three lobes.

Family STERNOPTYCHIDAE

Sternoptyx. The gas-gland is three-lobed, while the resorbent area lies between and beyond these lobes.

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[1] Pantin (1954) aptly calls such recognition 'aesthetic', as opposed to the analytical deductive methods that the systematist must eventually use.

Argyropelecus. The gas-gland surrounds the resorbent area which is on the floor of the swimbladder. The form of the swimbladder is ellipsoidal but approaches that of a sphere.

Polyipnus. The gas-gland is bilobed and the resorbent area lies between the lobes. In the adult the swimbladder is invested with fat.

It will be seen that certain swimbladder features, particularly the form of the gas-gland and its position relative to the resorbent area, can be used as diagnostic features in certain of the genera. Perhaps the associated circulatory system could also have been used; for instance, in the genera *Vinciguerria*, *Maurolicus* and *Pollichthys*. But the circulatory system can vary considerably within a genus and its species (see Godsil and Byer's (1944) study of the tunnies). Until more data are available it would seem best not to use the arrangement of blood-vessels as taxonomic characters.

Lastly, this survey has not been wide enough for much to be said on the distinguishing of species of deep-sea fishes by means of individual swimbladder structures. In one genus, *Gonostoma*, the three species are very unlike in this respect; I have already written (Marshall, 1950, 1954, 1955; Jones and Marshall, 1953) that *G. denudatum* has a normal type of swimbladder, that in *G. elongatum* the swimbladder regresses and becomes invested with fat, and that *G. bathyphilum* has no swimbladder. Differences of this order would seem, at first sight, to call for separate generic status for these three species. But reference to the papers just mentioned will show that there is a correlation between the degree of development of the swimbladder and the vertical distribution of each species. There seem to be parallel correlations in eye-structure, coloration (Marshall, 1954) and in other features (pp. 99–100). As closer study of such correlations is in progress, review of the status of the genus *Gonostoma* will be left until this work is completed. At present, however, there seems little justification for changing the present classification.

Suborder Salmonoïdea

The design of the swimbladder in the deep-sea salmonoids is very unlike that of the stomiatoids. The individual features are as follows: The swimbladder is euphysoclistous[1] (see footnote on p. 50) and the blood-vessels forming the retial system break up into numerous micro-retia, each consisting of a relatively small number (less than 50) of arterial and venous capillaries (or arterioles and venules). The gas-gland is diffuse rather than compact (Text-fig. 30 B).

The deep-sea salmonoids undoubtedly form a compact, natural group within the suborder Salmonoïdea. Günther (1866) placed *Argentina* and *Microstoma* in the Salmonidae and Brauer (1906) regarded *Winteria* and *Opisthoproctus* as other members of this family. Trewavas's (1933) anatomical study of *Opisthoproctus* properly revealed its salmonoid affinities, while the later work of Chapman 1942 a, b, 1943, 1948) clearly established the relationships between the above genera and *Rhynchohyalus*, *Bathylagus*, *Leuroglossus*, *Dolichopteryx* and *Macropinna*. More recently, Bertelsen (1958) has shown that *Xenophthalmichthys* is also an argentinoid fish, being closely related to *Microstoma* and *Nansenia*.

After Berg (1940) had introduced a new suborder (Opisthoproctoidei) for *Opisthoproctus*, Chapman (1942 b) subscribed to this opinion, but proposed that all the other genera should also be included in the new suborder (Berg puts them in the Salmonoïdea).

The swimbladder characters support Chapman's contention that *Opisthoproctus* should not be placed apart from the other deep-sea salmonoids. To Chapman's (1942 a) list of characters for his 'opisthoproctoid' fishes may be added those given above concerning the swimbladder. Furthermore, the similarities in the design of the swimbladder are so striking that some support is given to Hubbs's

[1] In *Argentina*, *Glossanodon*, *Microstoma* and perhaps in *Nansenia* the posterior part of the swimbladder is thin-walled and functions as the resorptive part of the sac. In *Opisthoproctus* and *Winteria* this part of the sac may also have this function, but the material available was not sufficient to confirm this suspicion.

(1953) idea of putting the deep-sea salmonoids into a single family, Argentinidae. (At present they are grouped into the families Argentinidae, Bathylagidae, Microstomidae, Xenophthalmichthyidae, Dolichopterygidae, Winteriidae, Macropinnidae and Opisthoproctidae.) While Hubbs may be wanting to make too great a leap in the other direction, there would seem to be good reason for regrouping of these fishes to give better expression of their relationships. Perhaps the suborder Salmonoidea might be split into the divisions Salmoniformes and Argentiniformes, the latter containing the deep-sea forms. The last four families, in parentheses above, could be united into one, Opisthoproctidae, following Hubbs's first suggestion in his paper, while *Xenophthalmichthys*, in view of Bertelsen's (1958) work, could be included in the Microstomidae.

Order *Iniomi*

When defining this order, Berg (1940) wrote that the swimbladder, if present, has a pneumatic duct. The only iniomous fishes with a swimbladder are the Myctophidae and *Neoscopelus* (see also Marshall, 1955) and these have a closed swimbladder. There is nothing resembling a pneumatic duct in the adult, although the 'oval' in the myctophids may perhaps arise from the posterior part of the larval connection between the gut and the swimbladder. Like the stomiatoids, the iniomous fishes were most probably derived from an early type of teleost fish with an open swimbladder, and as Tracy (1911) suggested, the oval may have been evolved by a progressive reduction of the pneumatic duct. At all events, it would be interesting to study the development of the 'oval' in a myctophid.

The swimbladder of iniomous fishes is very unlike that of the stomiatoids and salmonoids. It is physoclistous[1] with three to five retia mirabilia which originate at the anterior end of the bladder. As might be expected, the retia draw their blood from vessels that arise in front of the swimbladder. Each rete usually supplies a corresponding lobe of the gas-gland.

Suborder Myctophoidea

The myctophid swimbladder is definitely euphysoclistous, having at the anterior end of the sac an 'oval' type of resorbent surface. There are always three unipolar retia mirabilia supplying the gas-gland (see Text-fig. 30c). These individual features provide more evidence for regarding the myctophids as a compact monophyletic group, but the ancestor of the myctophids can hardly have been 'derived from Isospondylous stock very like the Gonostomatidae' as Fraser-Brunner (1949) supposed. The differences between the stomiatoid and myctophid swimbladders are very considerable as Table 1 shows.

Table 1. *Stomiatoid and myctophid swimbladders*

	Myctophidae	*Stomiatoidea*
Swimbladder type	Euphysoclist (with oval)	Paraphysoclist
Number of retia	Three	One
Type of rete	Unipolar	Bipolar
Position of rete	Anterior	Posterior

In view of this, it is unlikely that the specialized swimbladder of a stomiatoid could have been transformed into that of a myctophid. As already suggested, the Myctophidae were probably derived from an early generalized form of isospondylous fish. The common origin of the myctophid and stomiatoid lines of evolution would thus be further back in the early history of the teleosts.

[1] I was unable to determine whether *Neoscopelus* was a euphysoclist or paraphysoclist.

Neoscopelus

Apart from the uncertainty of its type of swimbladder, this genus is readily distinguished from all myctophids in the number of retia mirabilia, there being more than three retia (five in two individuals that were examined (Text-fig. 30 D). *Neoscopelus* has been classified within the Myctophidae, either as one of the genera, or as the type, of the subfamily Neoscopelinae (Fraser-Brunner, 1949). In many ways it is quite unlike the myctophids (*sensu stricto*), particularly in the arrangement and structure of the light organs (Brauer, 1908). Such differences, together with those found in the swimbladder, certainly indicate that the genus should be placed apart from the myctophids. As already suggested (Marshall, 1955), it might be better to put it into a separate family (Neoscopelidae) together with the genera *Scopelengys* and *Solivomer*.

Order *Miripinnati*

The basic features of the swimbladder of these fishes have already been described (Bertelsen and Marshall, 1956). In the sharp separation of an anterior thick-walled secreting part from a posterior thin-walled resorbent part, the organ is euphysoclistous, but there appears to be no diaphragm. The gas-gland receives its blood supply through two unipolar retia mirabilia that originate in the middle region of the sac and are formed from a posterior artery and vein (Text-fig. 30 E).

The only known oceanic fishes with two such retia mirabilia are *Anoplogaster* and *Stephanoberyx*, but in the latter genus, and in the Melamphaidae, the resorbent part of the swimbladder is formed by an oval.

Order *Allotriognathi*, Family STYLOPHORIDAE

The swimbladder of *Stylophorus* is readily distinguished from those of other pelagic, deep-sea fishes. It is euphysoclistous with a single unipolar rete mirabile receiving blood from an artery-vein pair that originates in front of the forward end of the sac. Unlike most euphysoclists, the front half of the swimbladder is provided with a resorbent capillary system, while the rear half contains the gas-producing glandular tissue (Text-fig. 30 F). The organ regresses during adult life.

Order *Berycomorphi*

The bathypelagic members of this group are mainly to be found in Regan's (1911) order Xenoberyces. The families are Stephanoberycidae,[1] Anoplogastridae and Melamphaidae. Parr (1929) also placed the Rondeletiidae in Regan's order, but Harry (1952) has provided ample evidence for regarding this family, together with the Barbourisiidae and Cetomimidae, as forming a 'natural group widely distinct from all other families of fishes...'. The three genera considered in this report, *Stephanoberyx*, *Anoplogaster* and *Melamphaes*, all have a closed swimbladder[2] with one or two unipolar retia mirabilia that originate at the posterior end of the sac.[3] In *Stephanoberyx* and *Melamphaes*, the swimbladder is definitely euphysoclistous, for an 'oval' is present (Text-fig. 30 G, H).

Regan (1911) decided that the Stephanoberycidae and Melamphaidae were sufficiently different from 'typical Berycomorphi' to be placed in a separate order, Xenoberces. They are also distinct in swimbladder characters. As we have seen, in *Stephanoberyx*, *Anoplogaster* and *Melamphaes*, there are one or two retia that originate at the posterior end of the swimbladder. In the Berycomorphi, as restricted by Regan, all available evidence shows that the retia originate at the anterior end of the sac (Rauther, 1922; Nelson, 1955).

[1] *Stephanoberyx* may be demersal rather than pelagic in habit.

[2] *Stephanoberyx* is said to have a pneumatic duct (Regan, 1911; Berg, 1940), but I was unable to find one.

[3] Dr A. Ebeling, who is revising the Melamphaidae, has been good enough to tell me that in certain melamphaids (*Melamphaes* s.s.) the retia are at the front of the swimbladder.

But such differences, together with those found by Regan, would hardly seem to require separate ordinal status. Regan himself felt that the Xenoberyces were 'probably derived from the same stock as the Berycomorphous fishes'. It would thus be preferable to regard the 'Xenoberyces' as a suborder of the Berycomorphi. The other fishes of this order (Regan's Berycomorphi) would form the other suborder.

The order Berycomorphi (*sensu lato*) may be defined as physoclistous teleosts with the anterior rays of the vertical fins spinous and with nineteen principal rays (seventeen of which are branched) in the caudal fin (eighteen principal rays with sixteen branched in the Polymixiidae). Pelvic fins sub-abdominal or thoracic, with or without a spine, and with three to thirteen soft rays. Mouth bordered above by protractile premaxillae; one or two supramaxillae. Orbitosphenoid present or absent.

Suborder Berycoidea: Families POLYMIXIIDAE, BERYCIDAE, DIRETMIDAE, TRACHICHTHYIDAE, MONO-CENTRIDAE, ANOMALOPIDAE, HOLOCENTRIDAE

Orbitosphenoid present; a subocular shelf usually developed, palate usually toothed one or two supra-maxillae (Regan, 1911). Swimbladder with retia mirabilia originating at the anterior end of the sac.

Suborder Anoplogastroidea: Families STEPHANOBERYCIDAE, MELAMPHAIDAE, ANOPLOGASTRIDAE[1]

No orbitosphenoid; no subocular shelf; palate toothless; a single supramaxilla, triangular in shape (Regan, 1911). Swimbladder with one or two retia mirabilia, usually posterior in position: an oval at the posterior end of the sac.

Order *Percomorphi*, Family CHIASMODONTIDAE

Like many other percomorph fishes, *Chiasmodon niger* has a euphysoclistous swimbladder with a diaphragm separating an anterior gas-producing chamber from a posterior resorptive chamber (Text-fig. 30J). Jones and Marshall (1953) and Fänge (1953) have drawn attention to percormorphs with this type of swimbladder.

To conclude, there is the problem of what the structural pattern of the swimbladder may add to present conceptions of the relationships between the major groups of deep-sea teleosts.

The Isospondyli undoubtedly contain the most generalized forms of teleosts. Although the fishes of each isospondylous suborder are specialized in varying degrees, they still retain certain characters of the early primitive teleosts. While the stomiatoids have special features, such as light organs, that are correlated with a bathypelagic mode of life, Regan (1923) looked on them as being quite similar to the clupeoids. He found the skull of *Photichthys* to be very like *Elops*, which is perhaps the most primitive of all living teleost genera. The extreme development of the gas-producing tissues of the swimbladder (or the complete loss of this organ) is also an adaptation to a deep-sea existence, but the structural pattern is quite unlike that in any other group, whether deep-sea or otherwise.

It is unlikely, as already stated, that the Myctophidae, with a very different form of swimbladder, were derived from a stomiatoid stock. In acquiring an oval, the myctophids have a remarkably advanced type of swimbladder relative to their position in the evolutionary scale of teleosts. Above the Iniomi, an oval is not encountered until the Anacanthini (cod-like fishes) are reached. However, an oval would seem to be no more efficient a resorbent surface than the capillary system in stomiatoids. *Astronesthes* is no more limited in its vertical migrations than the myctophids on which it feeds (see p. 88). From the functional as well as the structural aspect, the conclusion repeated in the first sentence of this paragraph seems to be justified.

[1] Grey (1955) has confirmed that *Anoplogaster cornuta* (Val) is the young of *Caulolepis longidens* Gill and also synonymizes the latter under the former (in accordance with the principle of priority in the International Rules of Zoological Nomenclature).

The Miripinnati and most Anoplogastroidea resemble the stomiatoids in having retia that are formed at the posterior end of the swimbladder, although both groups consist of euphysoclists, while all stomiatoids are paraphysoclists. The transformation of a stomiatoid type of swimbladder, with its unique vascular arrangements for the resorption of gases, to either the miripinnatous or anoplogastrid form would seem most unlikely. It is thus evident that the stomiatoids are a well-defined phyletic line of isospondylous fishes which, as the result of evolution in other directions, have left no living descendants.

Earlier discussion suggests this is also true of the deep-sea salmonoids. They are a compact, specialized group, forming a morphological (perhaps also an evolutionary) series towards forms like *Opisthoproctus*. However, the 'bauplan' of their swimbladder could very well have been derived from the more generalized condition seen in the salmonids.[1]
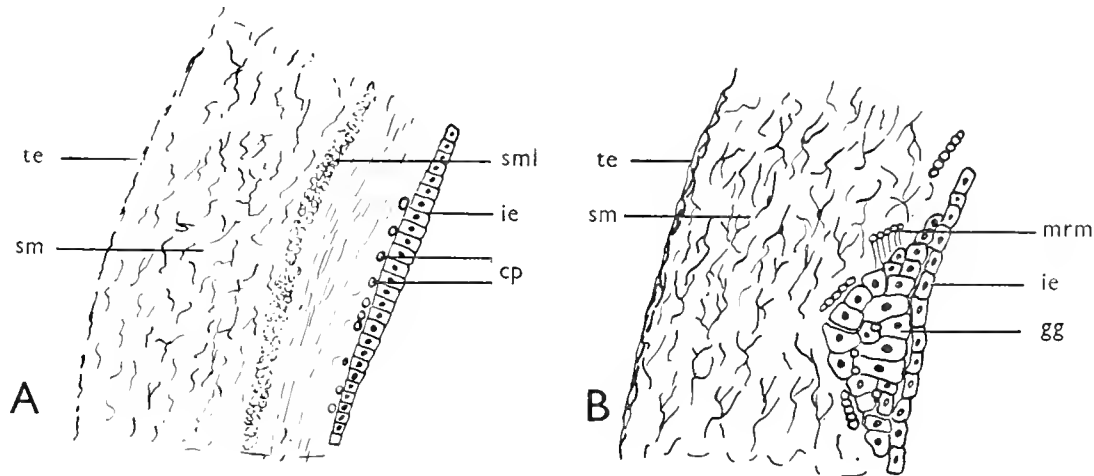
Text-fig. 31. Semidiagrammatic representations of transverse sections through the swimbladder wall of (A) *Salmo*; (B) *Opisthoproctus*. *cp*, capillaries; *ie*, inner epithelium; *gg*, gas-gland; *mrm*, micro-rete mirabile; *sm*, submucosa; *sml*, layer of smooth muscle; *te*, tunica externa.

In *Salmo* the swimbladder is supplied with arterial blood through branches of the coeliaco-mesenteric and intercostal vessels. Venous blood leaves through a vessel running forward to the portal system and through others leading to the intercostal and gonadial veins. The capillary stem may here and there form associations, but there is no regular development of retia mirabilia. The inner epithelium over the forward part of the sac, consists of columnar cells, elsewhere of flattened or cubical cells (Rauther, 1922). All that is required to turn such a swimbladder into the deep-sea salmonoid type is the regular association of capillaries to form micro-retia mirabilia, the differentiation of the inner epithelium to form gas-glands and, of course, the loss of the pneumatic duct. This may be better followed in Text-fig. 31, which shows semi-diagrammatic, transverse sections through the swimbladder walls of *Salmo fario* and *Opisthoproctus soleatus*.

The lineages represented by the orders Iniomi, Cetunculi, Chondrobrachii and Miripinnati may well have evolved from a common ancestor. Presumably this ancestral fish had advanced beyond the level of organization of the primitive Isospondyli (in that its premaxillae excluded the maxillae from the biting edge of the upper jaw and the mesocoracoid arch was lost from the shoulder girdle). The orders Giganturoidea and Lyomeri may also belong to this evolutionary complex (Bertelsen and Marshall, 1956).

The only fishes in these orders with swimbladders are the Myctophidae, Neoscopelidae (Iniomi), and the Miripinnati. The Myctophidae and *Neoscopelus* are considered to be rather closely related,

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[1] Fahlen (1959) has shown that there are (micro)-retia mirabilia in the swimbladder of *Coregonus lavaretus*.

and this, as we have seen, is supported by the similarities between their swimbladders. But there is little resemblance, other than that implied by the general label 'euphysoclist', between the miripinnatous and myctophoid type of swimbladder. Again, it would seem that the two groups are not closely related and that each is the result of a distinct evolutionary trend within the iniomous complex. But morphological knowledge of the various groups is by no means comprehensive. In time it may be possible to regard the Chondrobrachii, Cetunculi, Miripinnati and perhaps the Giganturoidea and Lyomeri as suborders of the Iniomi. At present their differences are more apparent than their similarities.

Whereas the Isospondyli are the basal group of soft-rayed fishes, the Berycomorphi occupy a similar position within the spiny-finned groups. These fishes have 'advanced' beyond the iniomous level of organization in the development of spinous rays in the vertical and pelvic fins. But like many of the soft-rayed fishes with a fully developed caudal fin, nearly all Berycomorphi have nineteen principal rays in this fin.

After their origin, the berycomorphs seem to have split up into two series of lineages, now represented by the suborders Berycoidea and Anoplogastroidea. The former group mainly consists of shallow and deep water fish, whereas in the latter the fishes are predominantly bathypelagic in habit. It is curious that like the stomiatoids among the Isospondyli, the purely deep-water group of berycomorphs acquired a swimbladder with a reversed polarity, the gas-secreting complex coming to a focus, as it were, at the posterior end of the sac. The differences between the stomiatoid and anoplogastroid swimbladder, to which some reference has already been made, are summarized in Table 2:

Table 2. *Swimbladder structure: Berycomorphi and Isospondyli*

Swimbladder	Isospondyli Stomiatoidea	Berycomorphi Anoplogastroidea
Type	Paraphysoclist	Euphysoclist (with oval)
Type of rete	Bipolar	Unipolar
Position of rete	Posterior	Posterior
Number of retia	One	One or two

As in the earlier comparison between the stomiatoids and myctophids, there is little reason to suppose that the second group might have been derived from the first. However, the berycomorphs may well have come from a primitive type of iniomous fish (in that its premaxillae alone formed the biting part of the upper jaw). The present-day representatives are all marine fishes and their evolutionary radiations, with the notable exception of the Holocentridae, have been mostly directed towards the deep ocean. Considering only marine teleosts, it looks as though some of the groups, that evolved during the early 'explosive' radiations of the soft-rayed and spiny-rayed teleosts, were 'edged out' from the more productive shelf-waters into the deeper, less favourable waters of the ocean.

As the common ancestor of both assemblages is likely to have had an open swimbladder, and as a closed one seems to be essential for an oceanic fish, it may well be that the physoclistous condition was independently evolved in the deep-sea Isospondyli and Berycomorphi. Furthermore, the same is probably true within the Isospondyli themselves, for it seems clear that the deep-sea salmonoids were derived from physostomatous stock (p. 55) and it is also evident that the stomiatoids were not part of this evolutionary line (p. 50). Again, the type of closed swimbladder possessed by the Myctophidae could well have been independently acquired. While the common ancestor of the soft-rayed and spiny-rayed groups must be sought at an early stage in teleost evolutionary history, the common factor in these developments of a closed swimbladder seems to be no more than residence in a living space in the deeper reaches of the ocean.

The larval swimbladder

The teleost swimbladder arises early in development as an outgrowth of the dorsal or lateral walls of the foregut. While the embryonic formation of the swimbladder in a deep-sea fish has yet to be described, the sequence of events is likely to be very similar to that in shallow water fishes. When considering the general features of myctophid larvae, Holt and Byrne (1911) mentioned that from a very early stage the roof of the swimbladder appeared to be darkly pigmented. It is also clear from Jespersen and Taning's (1926) figures that the early post-larvae of gonostomatid fishes have a well-formed swimbladder. In post-larval *Vinciguerria* and *Maurolicus* I found the swimbladder to be full of gas.

The presence of gas in the larval swimbladder raises an interesting question concerning the early functioning of the organ in the deep-sea environment. In many shallow water fishes the sac is first inflated by the larvae gulping in air at the surface and passing it down the larval pneumatic duct (which disappears during later development in physoclists). While the larval life of most bathypelagic fishes is passed in the surface-layers, it seems likely that the eggs are shed at deeper levels. Hatching may thus take place as the eggs float upwards from the depths. If so, many larvae could be far from the surface-film when the larval swimbladder is ready to be filled with gas.

However, McEwan (1940) found that, in *Hemichromis*, the connection between the larval swim-bladder and the gut never developed a lumen and, to make sure of the implications of this discovery, the early larvae were denied experimentally all access to the surface. In spite of this the larval swim-bladder became filled with gas. McEwen found that at one stage the lumen was obliterated by the swelling of highly vacuolated cells forming the inner epithelium. Having expanded to the limit, these cells suddenly collapsed to form a flat epithelium, after which gas appeared in the cavity. If such a mechanism is found in deep-sea fishes, it is obvious that the larvae need not seek the surface-film in order to initiate the use of the swimbladder as a hydrostatic organ.

At least five species of *Cyclothone* (*braueri*, *signata*, *microdon*, *pygmaea*, and *acclinidens*) must have a gas-filled swimbladder during their larval life, but after metamorphosis the organ regresses and becomes invested with fatty tissue. Presumably this is also true for other deep-water fishes with a fat-invested swimbladder in the adult phase. All such species will best be considered in a separate section (pp. 65–68). In the Miripinnati (Bertelsen and Marshall, 1956) and *Stylophorus*, the larval swimbladder also undergoes regression, but does not serve as an attachment for fat in the adult.

Lastly, all available evidence shows that bathypelagic fishes, without any trace of a swimbladder when adult, are also without a definite larval organ. (I have examined larval paralepidids, scopel-archids, and melanostomiatids without finding a swimbladder.) Furthermore, Bertelsen (1951) remarked that larval ceratioids, like the adults, have no swimbladder, but he suggested that 'gela-tinous tissue under the skin, which is present in all Ceratioid larvae in more or less well-developed condition, could be regarded as a floating organ'. More recently, Shelbourne (1956) has seen a corre-lation between the pelagic habit in fish eggs and larvae and the development of large subdermal spaces in the young stages. As these spaces seem to be filled with low density fluids derived from the yolk, they act as buoyancy chambers. It is clear from Shelbourne's figures that voluminous subdermal spaces are developed regardless of the presence or absence of a swimbladder in the larval phase. This is also true of bathypelagic fishes. Larval myctophids belonging to species with a well-formed adult swimbladder (e.g. *Benthosema glaciale*, *Hygophum benoiti*, *Myctophum punctatum*) have large subdermal spaces, particularly in the head region (see Taning's (1918) figures). Regarding fishes without a swimbladder, we have already referred to Bertelsen's findings in the ceratioids. It would

seem that the larval swimbladder is not sufficient to bring the specific gravity of the larva to that of the environment. 'Buoyancy tanks' are required as well.[1]

THE SWIMBLADDER WALL

Excluding the peritoneal investment, there are four main layers of tissue in the swimbladder wall: an outer, closely-knit fibrous layer; a middle, loosely-woven, fibrous tissue layer; a layer of smooth muscle fibres, and an inner epithelial layer. The outer layer is usually known as the tunica externa, while Fänge (1953) called the middle layer the submucosa, for in structure and position it is very like the layer of the vertebrate gut that already has this name. As Fänge (1953) has said, '...from an embryological and comparative anatomical point of view the teleostean swimbladder is nothing else than an isolated part of the digestive tube, although adapted to special functions'. The inner layer consists of pavement epithelium, which is locally differentiated to form the gas-gland.

The swimbladder lies outside the coelom, between the gut and the kidneys. It is retroperitoneal in position, but it becomes invested in varying degrees with peritoneal tissue. While the dorsal edge of the peritoneum usually runs along the lateral walls of the swimbladder, in some teleosts this limit lies above the organ (Freunde, 1938). Between the peritoneum and tunica externa, there may be a padding of loose, reticular, connective-tissue cells. Strands of connective tissue also run between the roof of the sac and the outer coat of the kidneys, which lies close to the swimbladder wall.

The peritoneal coat and the tunica externa are mainly formed of closely packed collagen fibres. The submucosa is by far the most voluminous coating of the swimbladder wall and it usually consists of a reticulum of loosely packed, collagen fibres within a gelatinous ground-substance (Saupe, 1939; Fänge, 1953). This layer is particularly thick under the gas-producing structures of the swimbladder. Between the submucosa and the inner epithelium there is a layer of smooth muscle cells which I have been able to identify in a number of the fishes considered in this report.

From this general outline we may turn to closer consideration of the swimbladder wall in certain deep-sea teleosts.

Family STERNOPTYCHIDAE, *Sternoptyx diaphana*

The fine structure of the swimbladder wall of this hatchet fish has been described by Nusbaum-Hilarowicz (1920), who divided the layers of tissue into three sections: outer, middle and inner. The outer section consists of two layers of long connective tissue fibres, the fibrillar axes of the topcoat being at right angles to those of the undercoat. From his plate VIII, fig. 9 it is evident that the fibres of the undercoat describe circular paths about the long axis of the sac. The middle section is a loosely-woven reticulum of fibres, which are delicately fashioned and form most of the wall-thickness. The cavities between the fibres hold a homogeneous and transparent substance, which is not stained by such dyes as haematoxylin or eosin. Nusbaum-Hilarowicz suggested that in the living animal this substance is probably a serous fluid. Undoubtedly this layer corresponds to what Fänge (1953) called the submucosa, and he remarked that, '...the submucosa often has a jelly-like, half-fluid consistency'. As is usual, the inner layer consists of flattened epithelial cells which are locally differentiated to form the gas-gland.

Argyropelecus

The histology of the swimbladder wall of *Argyropelecus hemigymnus* was also described by Nusbaum-Hilarowicz. There is an outer layer, presumably the tunica externa, consisting of long fibres with elongated nuclei, which for the most part are set across the long axis of the sac. Underlying this

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[1] It would be interesting to know whether pelagic fish larvae with a swimbladder have relatively smaller subdermal spaces than those without this organ.

circular layer is a thick layer (the submucosa) of fibres forming a loosely-woven reticulum. As in *Sternoptyx*, this fibre complex would appear to be developed within a gelatinous matrix. Last comes the inner, filmy coat of pavement epithelium.

Longitudinal sections were prepared of the specimen of *Argyropelecus olfersii* described on p. 20. The tissue composition of the walls is much like that of *A. hemigymnus*. Above the gas-gland, the roof has a thickness of 50–100μ, most of this consisting of the submucosa. The floor of the sac under the gas-gland is about three times as thick as the roof, but this swimbladder was in a very relaxed state. When the swimbladder is taut and in the steady state, the walls must be a good deal thinner, even remembering that the above measurements have been taken from tissues shrunken by preservation and subsequent preparation.

Family GONOSTOMATIDAE, *Vinciguerria attenuata*

The swimbladder taken for sectioning came from a fish of standard length 32·5 mm. The sac was well expanded, the major and minor axes measuring 7·5 and 2·5 mm. The gas-gland was flattened and well displayed, appearing much like that of the fish described on pp. 7–9.

Over the roof of the rear part of the swimbladder the walls measured about 20μ in thickness. There is a thin tunica externa formed of fibres running round the sac; then comes the reticulate submucosa which takes up most of the wall thickness. Near the rete mirabile the walls are padded with a voluminous submucosa measuring about 250μ in thickness. The swimbladder is lined with a filmy pavement epithelium.

Vinciguerri nimbaria

The swimbladder described on p. 9 was used in the preparation of serial transverse sections. It is of particular interest in that the sac was much contracted, but not collapsed, while the gas-gland formed a thick bunched-up mass.

The swimbladder is completely invested by a layer of peritoneum bearing many melanophores and formed of close-set fibres. The thin tunica externa is made up of circular fibres, while the very thick submucosa varies from 50 to 100μ in width. Owing to the relaxation of the sac, the fibres of the submucosa have been thrown into a series of undulations (see also p. 65).

Cyclothone

During the larval phase, the species of *Cyclothone* have a gas-filled swimbladder, which regresses and becomes invested with fat after metamorphosis to the adult. The development of the latter condition is dealt with in another section (pp. 65–68). Here we deal with the wall structure of the larval swimbladder.

The species of *Cyclothone* studied by Nusbaum-Hilarowicz (1920) was probably *braueri* and not *signata* (see p. 18). It is evident from his plate VIII that the swimbladder was in the larval condition, although fig. 3 shows a trace of the regular reticulate tissue (which holds the fat) at one end of the sac.

He found a thin but tough outer layer (tunica externa), consisting of long fibres that encircle the sac followed by another thin layer of rounded and branching cells. The next and median layer (submucosa) was very voluminous at the front and rear sections, but quite thin in the middle region. This was formed of fibrillar and loosely compacted tissue. The inner epithelial layer formed the gas-gland at the front of the sac.

Transverse sections through the swimbladder of a *Cyclothone braueri* of standard length 26·5 mm. revealed much the same tissue structure. The swimbladder has a length of about 3 mm. and around the gas-gland the walls have a thickness of from 100 to 200μ.

A 10-mm. larval stage of *C. pygmaea* from Thor station 144 was also sectioned. There is little that need be added, except to mention that the sac is completely invested with a densely pigmented

peritoneal coat. This is formed of strong close-set fibres that tend to run along the major axis of the swimbladder.

Astronesthes niger

The swimbladder described on p. 23 was examined under a high-power binocular, the tissue layers of the walls being teased apart. The sac is completely enveloped by the peritoneal coat, which is constructed of close-set fibres that are set along the major axis. The underlying tunica externa is formed of circularly disposed fibres. Next follows the thick submucosa with its loose network of fibres that run in all directions.

Family MYCTOPHIDAE, Myctophum punctatum

A swimbladder measuring about 12 mm. in length and 5 mm. in depth was sectioned.

The peritoneum extends round the floor and lateral walls of the sac. It is formed of lamellar collagen fibres (about $5-10\mu$ in width) which run along the major axis of the sac. This layer carries melanophores. The underlying tunica externa is barely detectable, but is comprised of fibres that run round the swimbladder. As is usual, the submucosa forms most of the wall thickness, this being about 300μ under the gas-gland and about 50μ in the roof of the sac. Remains of the ground substance could be seen adhering to the loose fibrillar network. Here and there the cells of the ground substance could be detected. Finally, there is a filmy coat of pavement epithelium lining the inner surface of the sac.

Diaphus rafinesquei

Certain details of the structure of the swimbladder wall have been described by Rauther (1922). As in *Myctophum punctatum*, the fibrous peritoneum ('fibrose hülle') does not completely invest the sac but extends rather more than half way up the lateral walls. Between the peritoneum and what Rauther drew as a thick circular layer of fibres is a padding of loose, reticular connective tissue. The circular layer must represent the tunica externa and the submucosa. Microscopic examination of the swimbladder of the fish from Discovery station 3484 (see pp. 30–32) revealed other structural details.

At least at the forepart of the organ, the peritoneal coat extends over the roof of the sac. It is formed of fine and close-set collagen fibres together with a number of elastic fibres. The tunica externa consists of relatively strong fibres running round the sac, while the more delicate fibres of the submucosa form a loose network. As far as could be judged the lateral walls are about 50μ in thickness, the submucosa accounting for about nine-tenths of this dimension.

To summarize, the wall of the swimbladder usually has this structure: a voluminous loosely-woven reticulum of collagen fibres in a gelatinous ground-substance separates the thin, but tough outer fibrous layer from the inner, filmy epithelium lining the sac walls. Clearly this tissue-complex must have adequate mechanical, as well as gas-proofing qualities.

In the steady state any loss of gas by diffusion out of the sac can be countered by the activity of the gas-gland. Presumably the walls will be under tension without undue strain. It would also seem likely that the fibres of the submucosa will lie close together within the gelatinous matrix, so forming a densely matted tissue, not the loose reticulum seen in prepared sections.

Concerning the gas-proofing qualities, a fish living at a depth of 500 m. will most probably have 80 per cent of oxygen in its swimbladder gases, so the swimbladder wall must contain a pressure of 40 atmospheres of oxygen against the tensions of this gas in the body fluids. (About 0·2 atmosphere for arterial blood.) Evidently, the swimbladder wall must be remarkably impermeable to oxygen.

MECHANICAL PROPERTIES OF THE SWIMBLADDER WALL

Apart from Alexander's (1959 a, b, c) studies of the swimbladder wall of cyprinid and other fishes, little is known of the physical properties of this tissue-complex. In cyprinids the posterior chamber of the swimbladder is remarkably inextensible, a property that is related to the high collagen content of the walls: the anterior chamber is more extensible (Alexander, 1959 b). The swimbladders of pike and trout are much more extensible and much weaker than cyprinoid swimbladders (Alexander, 1959 c). Judged by their fine structure, this is also true of the swimbladders of bathypelagic fishes in comparison with those of cyprinids.

Some preliminary notion of the physical properties of the swimbladder wall can be deduced from the observations of Scholander, Claff, Teng and Walters (1951) and Jones (1952). These workers considered how far a closed swimbladder might restrict rapid vertical movement in a fish above a certain level—the level at which it was in hydrostatic equilibrium. Scholander and his colleagues suggested that a fish would not move upwards beyond a level involving more than a 25 per cent change in the volume of its swimbladder, which is in good agreement with Jones's figure of 22 per cent.

An increase of 25 per cent in the volume of a swimbladder will not lead to more than a moderate extension of the walls. As this figure may well apply to deep-water pelagic fishes, we may briefly consider what would happen to the ellipsoidal swimbladder of a myctophid. (A fish with a standard length of 70 mm. will have a swimbladder with a volume of about 0·25 ml.) An increase of 25 per cent in the volume will be accompanied by rather less than 10 per cent increase in the lengths of the major and minor axes, assuming the walls are uniformly elastic and the sac is free to expand.

There is a further consideration: when fully expanded, the oval is by far the thinnest part of the swimbladder of a myctophid, and during the hauling of a fish to the surface, the oval may be blown out in the form of a blister. (This condition was found in several specimens of *Myctophum punctatum* and *Diaphus rafinesquei* (see Text-fig. 15 d). Taking an oval with the walls distorted in the form of a hemisphere, the surface area will be increased by a factor of two. If this amount of expansion can be sustained by the flimsiest part of the swimbladder, it is unlikely that the limitation of rapid upward movements is set by the range of extensibility of the walls. (In *Argyropelecus* also it is clear that the swimbladder can sustain more than a 10 per cent increase in the lengths of the major and minor axes.) The restriction is more likely to be related to the fishes' incapacity to cope with more than a certain decrease in its density, there being a limit to what can be done by compensatory movements of the fins and body.

Whatever may be the limits of extensibility, it is rare to find a bathypelagic fish with a burst swim-bladder or ruptured body-wall. While it may be easy to miss a small hole in the swimbladder of a preserved fish, distension of the organ (so that the viscera are forced out of the mouth or anus) is also unusual, except perhaps in hatchet fishes (see also p. 95).

In a letter Dr F. R. Harden Jones has told me that perch (*Perca fluviatilis*) with burst swimbladders do not appear to have ruptured body-walls, although in some instances the pressure may be sufficient to evert the rectum. Out of a sample of 106 cod taken by trawl at 20 fathoms, he found 45 per cent with broken swimbladders. At greater depths (30 fathoms and above), all were broken. But there is no evidence that the swimbladder walls of vertically migrating deep-sea fishes are any tougher in relation to the size of the sac than those of perch or cod. Saupe (1939) gives 250–300 μ as the thickness of the walls in the perch, but makes no mention of the size of the fish. This may be compared with the measurements (20–300 μ) given earlier in this section, for various species of stomiatoids and myctophids. Furthermore, there is no indication that the collagenous elements in the swimbladder wall of bathypelagic fishes are more closely packed than those of shallow water species.

Perhaps these differences between perch, cod and bathypelagic teleosts have a functional rather than a mechanical basis. A cod being hauled to the surface in a trawl is subjected to pressure changes beyond those it normally experiences. This would not apply to those bathypelagic fishes which migrate upward each day to the surface-waters. However, discussion of this will best be left to the section dealing with gas resorption (pp. 78–81).
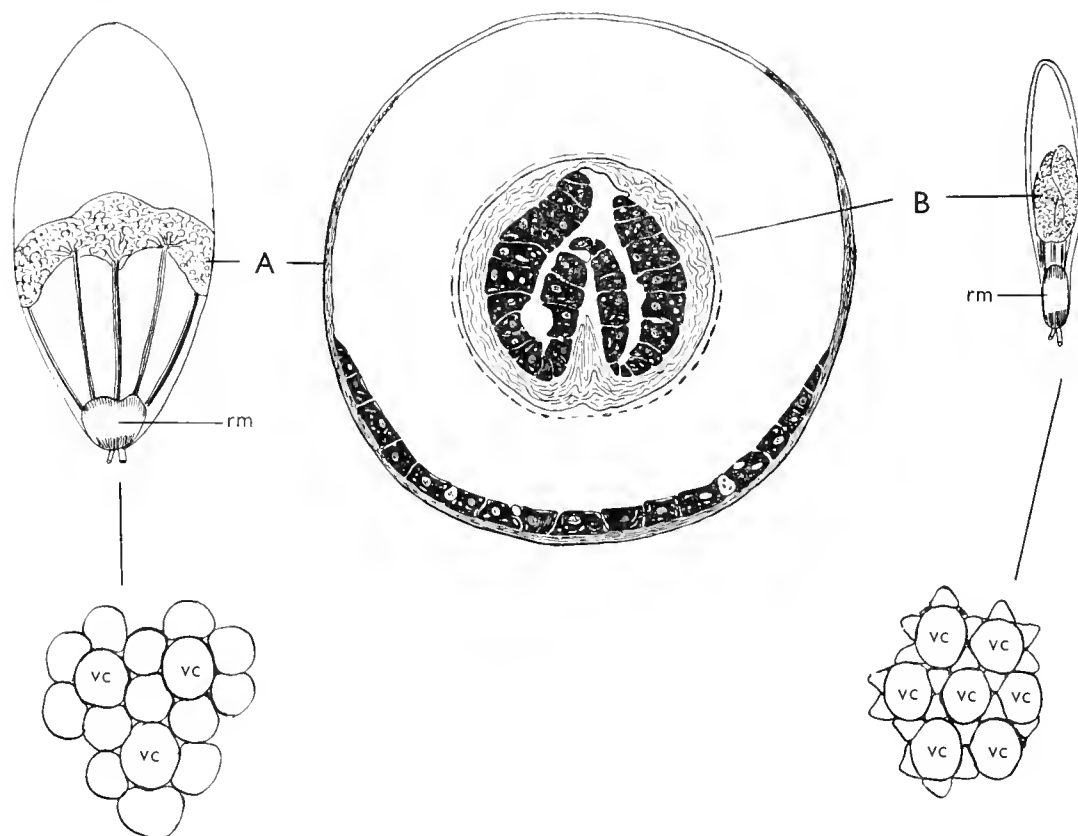
Text-fig. 32. Semidiagrammatic reconstructions of the swimbladder of *Vinciguerria* in (A) an expanded, and (B) a compressed state. Note the changes in shape of the gas-gland cells (shown black) and the retia mirabilia (*rm*). The undulating patterns in the submucosa of the compressed swimbladder may be better seen in the microphotograph in Pl. I, fig. 1. Below are shown cross-sections of the capillaries of the retia (*vc*, venous capillaries, others arterial). In those belonging to (A) both sets of capillaries are expanded, as during gas secretion: in (B) the arterial capillaries are occluded, as during gas resorption.

During the migration of a fish towards the surface, the physical properties of the swimbladder wall must be adequate to withstand any stresses that might arise. But the walls will presumably be under tension without undue strain. It would also seem likely, as we have said, that the fibres of the submucosa will lie close together within their gelatinous matrix. When the fish dives to its daytime level, certain evidence suggests that the swimbladder cannot be kept at the required volume in the face of pressure gradient (p. 91). As the swimbladder is compressed the volume of the fish will decrease and it would seem desirable that the tissues of the walls should be freely adjustable as the sac decreases in size. If, for instance, the connective tissues were 'rigid', with little play, kinks would appear in the wall which might eventually lead to one part of the delicate gas-gland being forced against another (see Text-fig. 32). However, the presence of a voluminous, semi-fluid submucosa will allow the tissues to relax in a uniform manner and so the swimbladder may keep its shape. In a large *Diaphus rafinesquei*, the swimbladder submucosa is about 150μ in thickness, and in a sac with major and minor axes of 12·0 and 7·0 mm., the volume of this tissue will be rather more than one-tenth of that of the gas.

If the sac is compressed to half its buoyant capacity, the volumes of the gaseous and gelatinous phases will differ by no more than a factor of five. This assumes that the volume of the submucosa is unchanged. But according to Le Chatelier's theorem, colloidal gels may be expected to take up more water if subjected to an increase in pressure (Johnson, Eyring and Polissar, 1954). At all events, a study of this aspect would be of interest.

Some indication of the flow-patterns in the submucosa of a compressed swimbladder was found in *Vin-ciguerria*. Sections were cut through two swimbladders, one of which was well expanded, the other completely relaxed. These are shown in Text-fig. 32 and Pl. I, fig. 1. The lines of flow are indicated by the undulations of the fibres in the submucosa. The great change in the shape of the gas-gland cells can also be seen. While looking at these sections I was reminded of the experiments described by Le Gros Clark (1945). An inflated rubber balloon, the surface of which was lightly oiled, was coated with a plastic material, such as gelatin or collodion. As the balloon was deflated, small elevations appeared on the surface of the plastic, each of which sent out a triradiate pattern of anticlines as the contraction proceeded. Such elevations were found in the submucosa of the relaxed swimbladder (see Pl. I, fig. 1) and under each were arches of fibres, looking not unlike the strata forming an anticline in the earth's crust.

Turning finally to the gas-proofing properties of the swimbladder wall, Fänge (1953) has clearly shown that it is the 'secretory mucosa' which is impermeable to gases. The secretory mucosa is the inner epithelium of the secretory part of the sac. During gas-production this tissue is in a relaxed state and covers the inner surface of the bladder (the resorbent part being contracted). It is hardly surprising that this should be so, for the other parts of the swimbladder carry many blood-vessels through which gases would be lost.

Evidently the inner epithelium is the 'inner tube', the connective-tissues being merely the 'tyre'.

FAT-INVESTED SWIMBLADDERS

The presence of a fat-invested swimbladder in a deep-sea fish was first discovered by Ray (1950). In her study of the peripheral nervous system of the myctophid *Lampanyctus leucopsarus*, she figures (pl. 12, fig. 30) a transverse section through the trunk at the level of the swimbladder. Like a normal gas-filled organ, it lies immediately below the kidneys and is surrounded by peritoneum, which is darkly pigmented, as is usual in deep-sea fishes. The organ is filled with reticular connective tissue having all the appearance of a system of fat-storing cells. Barham (1957) has given these further details: 'In the adult state the bladder is largely filled by fatty connective tissue. A well developed gas-gland is present and almost fills the reduced lumen, but in some specimens a gas bubble may be present.' He also records that another myctophid, *Diaphus theta*, has a similar type of swimbladder.

As already stated in the descriptive section, fat-invested swimbladders are found in a number of bathypelagic fishes. These are:

Suborder Stomiatoidea: Family GONOSTOMATIDAE, *Cyclothone* spp., *Gonostoma elongatum*; Family STERNOPTYCHIDAE, *Polyipnus laternatus*; Family ASTRONESTHIDAE, *Borostomias antarcticus*; Family STOMIATIDAE, *Stomias colubrinus*, *S. affinis*. Order *Berycomorphi*: Family ANOPLOGASTRIDAE, *Anoplo-gaster longidens*.

Kotthaus (1952) has also found a well-formed fat-bearing swimbladder in another deep-sea beryco-morph, *Hoplostethus islandicus* (family Hoplostethidae).

It will thus be seen that fat-invested swimbladders are found in deep-water fishes belonging to seven different families and three orders.

As already mentioned, the post-larval stages of *Cyclothone* have a small gas-filled swimbladder. It is after metamorphosis that the swimbladder regresses and becomes invested with adipose tissue. In

Cyclothone braueri metamorphosis occurs at a length of from 11 to 14 mm. (Jespersen and Tåning, 1926), but two individuals of lengths 17 and 26·5 mm. (St. 3094, 1500(-o) m., 21. v. 54) still had no deposit of fat around the swimbladder. However, in another fish of length 26 mm. there was a small cushion of adipose tissue at the anterior end of the sac. In a 31-mm. fish the larval swimbladder had lost its ellipsoidal shape and appeared as a glistening white sphere (with a diameter of o·6 mm.) in the middle of a blimp-shaped mass of fat, having a length of about 3 mm.
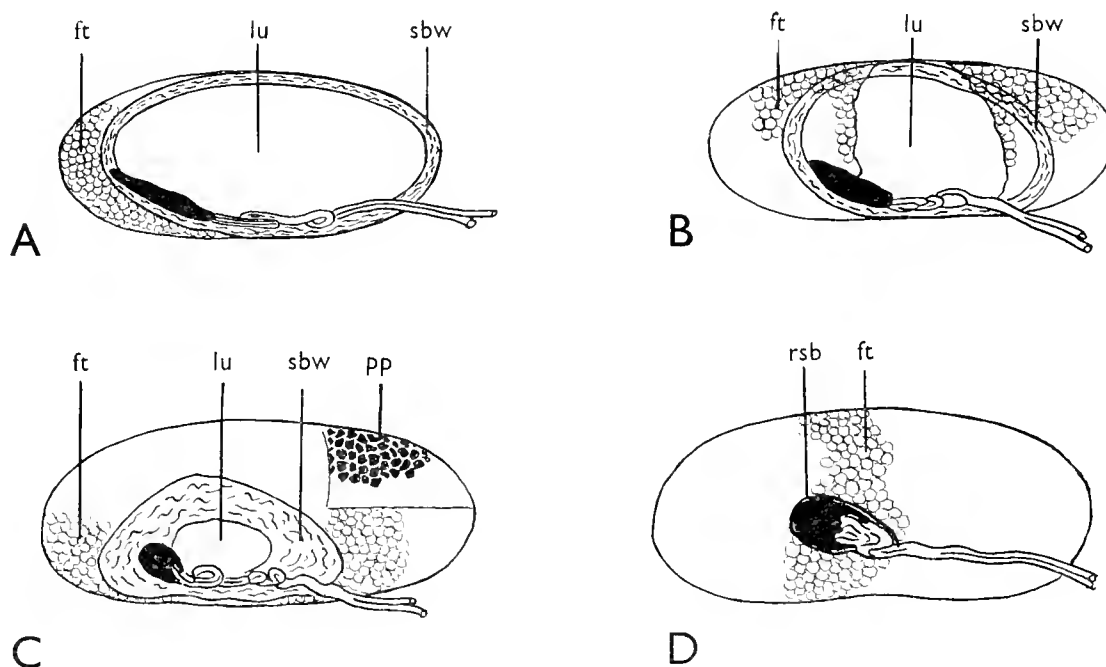
Text-fig. 33. Diagrammatic reconstructions of four stages (A–D) in the fatty investment of a regressing larval swimbladder in *Cyclothone livida*. The gas-gland is shown black. *ft*, fatty investment of swimbladder; *lu*, lumen of swimbladder; *pp*, pigmented peritoneum; *rsb*, regressed swimbladder; *sbw*, swimbladder wall.

Above and below the vertical diameter of the sphere, there was only a thin covering of fat. Finally, in a 56-mm. individual the remnants of the larval swimbladder measured no more than o·15 mm. in diameter and needed to be carefully looked for in its fatty investment. It would thus appear that the swimbladder is fully adipose in adults of about 35 mm. and upwards.

In *Cyclothone livida* (also from St. 3094) the sequence of changes is much the same and is summarized in Text-fig. 33. As in *C. braueri*, the larval swimbladder was completely regressed and surrounded by a sausage-shaped mass of fat when the fish had reached a length of about 37 mm.

This most advanced stage in the development was examined microscopically. In Text-fig. 34 is a drawing of a transverse section at the level of the regressed swimbladder (see also Pl. I, fig. 2). The left-hand figure shows the reticular system of fat-storing cells surrounding the central regressed part of the larval swimbladder. This part is shown enlarged on the right. An outer fibrous layer encloses a mass of regressed gas-gland cells, mostly without nuclei, and the remnants of the retial capillaries. The remaining space is filled up with fine loosely-woven reticular tissue, which is undoubtedly the remains of the submucosa. The tunica externa must be represented by the outer fibrous layer, which has much the appearance of the outer circular layer fibres described by Nusbaum-Hilarowicz (1920). The mass of fat-charged cells is almost entirely bounded by the darkly pigmented peritoneum with its fine mosaic of melanophores. Thus the fat is deposited between the peritoneum and the tunica externa and in this way comes to invest the larval swimbladder as it regresses.

Varying degrees of adipose tissue investment have been found around the swimbladders of adults of the hatchet fish, *Polyipnus laternatus*. This is shown in Text-fig. 35.

The top drawing represents a swimbladder from a 32·5-mm. fish and the sac has a relatively thin layer of fat around it. The middle and lower swimbladders came from 26·5 and 33·5-mm. fishes. In these the swimbladder is buried in a mass of fat, the outline of which has some congruence to that of the sac. As in *Cyclothone*, the fat was surrounded by darkly pigmented peritoneum.
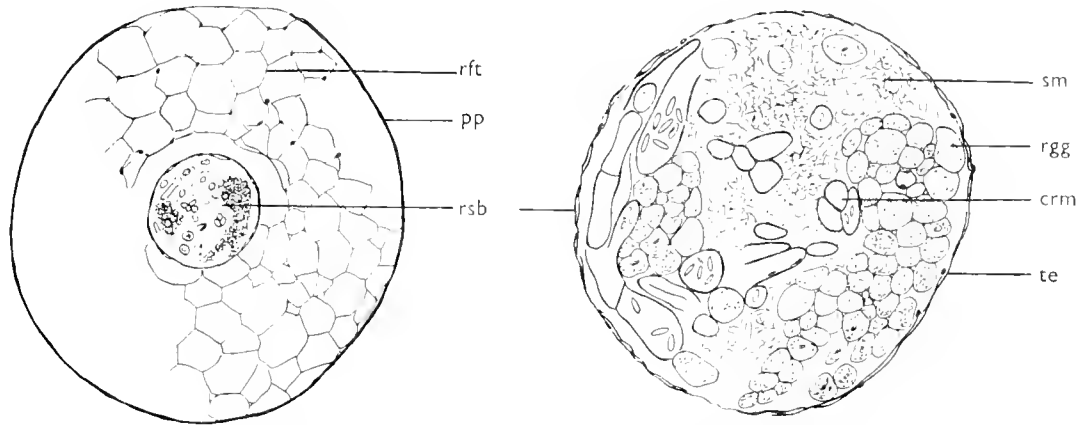
Text-fig. 34. Cross-sections through the fat-invested swimbladder of *Cyclothone livida*. On the left is shown the reticular fat-charged tissue surrounding the regressed swimbladder, which is shown enlarged on the right and has a diameter of about 300μ. *crm*, remains of capillaries of rete mirabile; *pp*, pigmented peritoneum; *rft*, reticular fatty-tissue; *rsb*, regressed swimbladder; *rgg*, regressed gas-gland cells; *sm*, submucosa; *te*, tunica externa.
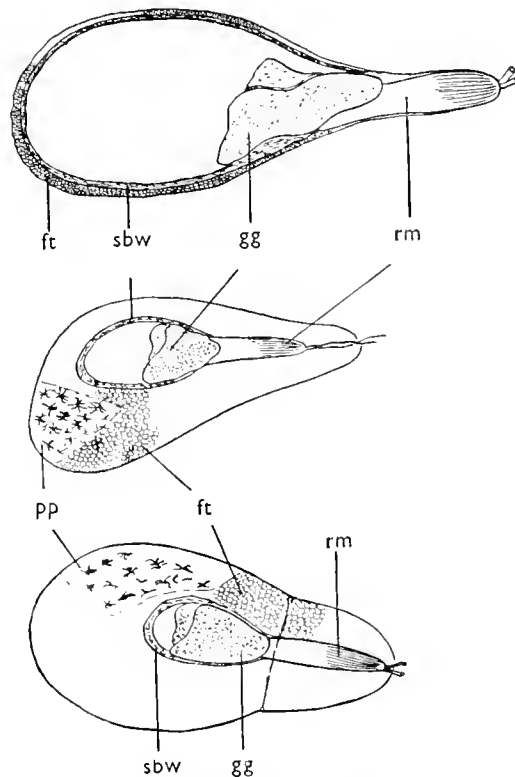
Text-fig. 35. Different degrees of fat-investment of the swimbladder of *Polyipnus laternatus*. The top swimbladder (× 7·5), showing the least degree of investment, is from a fish of standard length 32·5 mm. The middle one (× 8) comes from a 26·5-mm. fish, while the bottom one (× 6) is from a 33·5-mm. specimen. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *pp*, pigmented peritoneum; *rm*, rete mirabile; *sbw*, swimbladder wall.

Compared with the swimbladder of the 32·5-mm. fish, those of the other two fishes are considerably regressed, although the main features can be clearly distinguished. It is probably significant that the dimensions of the fat body surrounding the swimbladder of the 33·5-mm. fish are much the same as those of the swimbladder of the 32·5-mm. individual. It would seem that as the swimbladder regresses, the space left between the peritoneum and tunica externa is filled with fat. But the marked difference between the swimbladders of these two equal-sized fishes suggests there must be wide variability in the stage at which this regression begins to occur.

A hydrostatic organ consisting entirely of fat is superior to one containing gas in that fats are relatively incompressible. However, fats are not much lighter than sea water, having a density of about 0·9. In a marine fish the volume of gas-filled swimbladder need only be 5 per cent of the body volume to make the fish weightless in water (Jones and Marshall, 1953). But a marine fish without such an internal float requires about 30 per cent of fat by weight for neutral buoyancy. Clearly the replacement of gas by fat is an inadequate substitution, so far as buoyancy is concerned. In *Gonostoma elongatum*, Denton and Marshall (1958) found relatively little fat, the more significant fact being that this species almost achieves neutral buoyancy by having reduced muscular and skeletal systems. But in *Cyclothone*, as will be shown later (p. 103), there is, in addition to the fat investing the swimbladder and deposited in the mesenteries, a well-developed system of fat sinuses under the skin. In a well-fed *Cyclothone* these stores of fat may occupy up to 15 per cent of the body volume (about 13 per cent of the body-weight assuming the fish to be neutrally buoyant). Again, the more significant feature, particularly in a poorly nourished fish, is the reduction of the heavy muscular and skeletal tissues.

The following conclusion seems apt: In a number of bathypelagic fishes the swimbladder regresses after metamorphosis and becomes a convenient site for the deposition of fat, but this plays a relatively small part on the 'credit' side of the 'buoyancy balance sheet'.

THE SWIMBLADDER AS A HYDROSTATIC ORGAN

The teleost swimbladder acts as a hydrostatic organ by making the fish weightless in water. Whatever movements the fish may make, whether up or down, the nervous control of the swimbladder is such that it continues to function towards this 'desirable' end. In terms of cybernetics, the 'feed-back' is arranged to steer this system towards this 'goal', the weightless condition. In other terms, here is what the fishes told the diver in one of Isak Dinesen's (1958) 'simple' stories: 'We fish rest quietly, to all sides supported, within an element which all the time accurately and unfailingly evens itself out. An element which may be said to have taken over our personal existence, in as much as, regardless of individual shape and of whether we be flatfish or roundfish, our weight and body is calculated according to that quantity of our surroundings which we displace.'

Knowing the density of the tissues (about 1·076), it can be shown that the volume of the swimbladder in a marine teleost must be about 5 per cent of the body-volume if the fish is to be in hydrostatic equilibrium with the sea (Taylor, 1921). Measurements of this percentage volume in shallow water species closely agree with this theoretical figure (Jones and Marshall, 1953). Furthermore, Kanwisher and Ebeling (1957) have found a similar agreement in bathypelagic teleosts, their measurements of the swimbladder volume in various stomiatoids, myctophids and melamphaids ranging from 3·2 to 6·5 per cent of the body-volume. If deprived of their swimbladders, these deep-water fishes would need to sustain a downward force equivalent to 3·2–6·5 per cent of their weight in air in order to maintain themselves at a constant depth. Calculations made by Denton and Shaw show that the energy 'saved' can be quite appreciable (Denton and Marshall, 1958). Yet some energy is required to keep the swimbladder inflated at the appropriate volume and the amount is directly related to the

depth (Parr, 1937; Kanwisher and Ebeling, 1957), but in absolute terms this amount may be quite small (see p. 84). However, many of the bathypelagic fishes with swimbladders undertake daily vertical migrations. These will be considered in a later section (pp. 85–95). Here the main concern is with the structures involved in maintaining the swimbladder as a hydrostatic organ. These are the gas-secreting complex (rete mirabile and gas-gland) and those allowing of the loss of gases from the swimbladder (the resorbent capillary complex).

THE GAS-PRODUCING COMPLEX

The swimbladder produces gas by means of a capillary system supplying a glandular area. The gland is formed by localized modification of the epithelial cells that line the sac.

In physoclists and some physostomes (e.g. cyprinids, pike and eels) the capillaries form retia mirabilia. These consist of regular and intimate intercalations of arterial and venous capillaries, which follow parallel courses and carry blood to and from the gas-gland.[1]

The retia mirabilia

Some account of the form and size of the retial system has already been given in the descriptive part of this report (pp. 7–50). In this section the emphasis will be on the fine structure.

Woodland (1911 a, b) was the first to appreciate the essential features of retia mirabilia. He divided them into two types, unipolar and bipolar. In both kinds, an artery and vein subdivide to form the close and regular association of capillaries, (which may number many thousands), that supply the gas-gland. Before entering the gland, the retial capillaries of the bipolar type recombine to form arteries and veins, these then breaking up within the gland to form the capillary circulation. In the unipolar type the retial capillaries merely continue into the gland.

Both kinds of retia are found in the swimbladders of deep-sea fishes. All stomiatoids have a single, bipolar rete mirabile: the myctophids have three unipolar retia. Now some species of both groups live under similar hydrostatic pressures and undertake daily vertical migrations, and on this account, there would appear to be 'nothing to choose' between the efficiency of both types of system.

Apart from this consideration, it is interesting that the two most diverse groups of pelagic, deep-sea fishes, the stomiatoids and myctophids, differ in this particular way. However, it will be as well to remember Pantin's (1951) observation: that given certain standard parts, the number of structural solutions to a physiological requirement is limited by the nature and number of these parts. In this instance, given an artery and a vein that form a retial system, there would appear to be only two ways this system could feed a gas gland. The retial capillaries can either continue into the gas-gland (unipolar retia) or combine to form larger vessels (bipolar retia) before doing so.

The nature of the swimbladder as a whole must also be considered. Woodland (1911 a) and Fänge (1953) have shown that the retia mirabilia of teleosts with a euphysoclistous swimbladder are unipolar in type. This survey has provided further evidence for this generalization. Besides the Myctophidae, the other bathypelagic euphysoclists are the Miripinnati, Anoplogastroidea, *Stylophorus* and *Chiasmodon*. All these fishes have unipolar retia. At least some of the deep-sea salmonoids are euphysoclists and their micro-retia run straight to the gas-gland. This is hardly surprising.

Apart from the stomiatoids, the only other fishes known to have bipolar retia are the eels (Apodes). The development of a bipolar retia system in the first group would appear to be linked to the venous part of the resorbent area, which drains into vessels that also supply the gas-gland. Such a circulation would hardly be feasible with the unipolar type of rete (see also p. 78). However, in both euphysoclists and eels, the secretory and resorbent parts have their own circulatory systems (Fänge, 1953).

[1] In view of this association in parallel, the noun *rete* is quite inappropriate, but the adjective is justified, for these capillary systems are wonderful instances of biological engineering in miniature. A better name would be *fascis mirabilis*.

This being so, euphysoclists simply require unipolar retia, but the eels are an exception to this 'rule'. It should also be stressed that a bipolar retial system is not a characteristic of all paraphyso-clists. Unlike the stomiatoids, other teleosts with this type of swimbladder (Synentognathi and Microcyprini) have unipolar retia.

Turning now to the composition of the retia, Krogh (1922) was the first to appreciate the extra-ordinary extent of the capillary elements. In a cross-section of the two retia of the freshwater eel he estimated that there were 88,000 venous and 116,000 arterial capillaries. As the two retia were 4 mm. in length this gave aggregate lengths of 352 and 464 m. for the two sets of capillaries. Krogh also pointed out that the capillary elements are remarkably long compared to those in muscles, which are otherwise among the longest in the vertebrate body (e.g. 4 mm. in eel retia against 0·5 mm. in muscle).

Similar data are given in Table 3 for various species of bathypelagic fishes (see Pl. I, figs. 3 and 4 for the appearance of a rete in cross-section). The significance of the r/v ratio will become apparent in the text which follows.

Table 3. *Retial length : swimbladder volume ratios*

Species	Number of retial capillaries	Retial length (mm.)	Total length of capillaries (m.)	Total r/v = retial length : volume (ml.) of sac
Eel (*Anguilla anguilla*)	204,000	4·0	816·0	30
Argyropelecus aculeatus	5,000	2·0	10·0	50
Polyipnus laternatus	7,000	3·0	21·0	100
Vinciguerria nimbaria	5,000	1·0	5·0	150
Myctophum punctatum	2,000	2·5	5·0	20
Melamphaes megalops	500	12·0	6·0	30

At first sight the figures for the total lengths of the retial capillaries seem low compared with Krogh's 816 m. for the freshwater eel. But as the retia are an essential part of the gas-producing mechanism, their numerical constitution will be best regarded in relation to the volume of the swim-bladder. (The volume of the eel swimbladder was estimated from Fänge's (1953) fig. 17, assuming the secretory sac to be a perfect ellipsoid.) In view of this, an r/v ratio was calculated (r being the total length of the retial capillaries, and v the volume of the swimbladder (ml.)).

While these figures can only be rough approximations, it will be seen that, except for *Polyipnus* and *Vinciguerria*, the r/v ratio of the eel is much the same as those of the bathypelagic species. And in comparing these data, it should be remembered that during its reproductive migration the freshwater eel becomes a deep-sea fish. The agreement between the ratios is thus not altogether surprising. But before considering this problem further, reference must be made to Scholander's (1954, 1958) theoretical study of the rete mirabile of deep-sea fishes.

Following earlier suggestions, Scholander convincingly argued that the retia must form a counter-current system allowing of gaseous exchange between the arterial and venous capillaries. Without intimate contact between the two sets of vessels, the blood leaving the gas-gland would be continually removing oxygen from the swimbladder. He wrote as follows in his 1958 paper (page 7):

The atmospheric oxygen which is dissolved in the sea water has a gas pressure of no more than one-fifth of an atmosphere at any depth, and the arterial pressure in the fish is slightly below this. So across the thin swimbladder wall of a fish living at a depth of 2000 m. there is a drop in oxygen pressure of nearly 200 atmospheres. The swimbladder is a living organ and is circulated with blood. At a pressure of 200 atmospheres the blood becomes charged with ten times its own volume of oxygen by simple physical solution, and if such amounts were to leave the swimbladder there would soon be no oxygen left. In more

general terms, one may state the problem thus: How can a steep concentration gradient be maintained across a barrier in spite of the fact that liquid is continuously streaming through it? The answer lies in the arrangement of the vascular channels.

Clearly, the retia will be most efficient in gaseous exchange if the capillary elements fit together so as to obtain the greatest possible surface of contact. Scholander (1954, 1958) had some interesting observations on this aspect. Transverse sections through the retia of a deep-sea eel (*Synaphobranchus*), a rose-fish (*Sebastes*) and a rat-tail (*Coryphaenoides*) showed that the arterial and venous capillaries fit together to form either a chequer-board[1] or a hexagonal star pattern. The eel has the first arrangement, one giving the maximum gaseous diffusion between the afferent and efferent capillaries, and Scholander (1954) went on to say '...it is remarkable that we find it in our deepest fish. The only other solution to the topological problem of making four polygons (black or white) meet at one point in such a way that black always borders white is realized in the hexagonal star pattern found in the rete of the rosefish' (and in that of the rat-tail).

While looking through serial transverse sections of the swimbladder of various stomiatoids, *Argyropelecus aculeatus*, *Vinciguerria nimbaria* and *Polyipnus*, I found both types of pattern in the same rete. In *Polyipnus*, for instance, there is a transition from the hexagonal to the mosaic arrangement in passing from the proximal to the distal end of the rete (see Pl. I, fig. 4). At the beginning of the rete the arterial capillaries are occluded and form an hexagonal pattern round the larger (6–8μ) venous capillaries. About half-way down the rete, the arrangement is much the same, except that the arterial capillaries are partly open. Lastly, over the distal third of the rete, the two sets of capillaries form a mosaic pattern and are equal in size (6–7μ). In the specimen of *Argyropelecus aculeatus*, except for a middle area at the proximal end, the rete showed a hexagonal star pattern throughout.

In a specimen of *Vinciguerria attenuata*, however, the rete of which was well expanded, the capillaries formed a mosaic pattern at all levels (see Text-fig. 32a). The seemingly curious mixture found in other stomiatoid retia is likely to be no more than a reflection of the unique arrangement whereby venous blood from the resorbent capillary bed returns through the rete (p. 79). During the secretory phase the rete will be fully expanded and both sets of capillaries will then form a mosaic pattern. When gases are being lost from the swimbladder the arterial capillaries must be closed, while the venous elements will be fully expanded. In this way a hexagonal pattern would be formed. The mixture of patterns found in some retia would thus be due to the physiological state of the fish when it died in the net. Preservation and fixation might also play some part, but evidently not in the rete of *Vinciguerria attenuata* mentioned above.

In the Myctophidae, the vascular system of the oval does not involve the retia, other than that the arterial blood may come from a branch of the retial artery. In two species, *Myctophum punctatum* and *Diaphus dofleini*, transverse sections through the retia showed the capillaries to be rounded rather than polygonal, the appearance being more like a system of condenser tubes than a mosaic. In the living fish, their shape may be otherwise.

Apart from the intimacy of their association, the total surface of contact between the capillaries will obviously be directly proportional to their length. And an increase in length will not only lead to increased exchange of gases, but also slow down the rate of blood-flow and so further enhance the efficiency of the exchange. But before considering this aspect in bathypelagic fishes, some mention must be made of Scholander's (1954, 1958) concept of the rete as a device for the building up of high pressures.

Assuming that gases are liberated from the blood, Scholander derived an equation, showing that

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[1] 'Mosaic' would be a more apt descriptive term.

the equilibrium pressure is directly proportional to the diffusion across the retial capillaries and the amount of oxygen dissociated from a unit volume of blood. The inverse terms in the equation are the blood solubility coefficient for oxygen and the rate of blood-flow in the retial capillaries. Again, the longer the retial capillaries the greater the diffusion and the less the blood-flow, both of which will enhance the build-up of equilibrium pressures. Theoretically, a small difference in gas-tension in the arterial and venous capillaries at the beginning of the rete could lead to pressures of several thousand atmospheres at the end near the gas-gland. However, active secretion of oxygen by the gas-gland accords better with present knowledge than a liberation of this gas from the blood (Scholander, 1954; Sundnes, Enns and Scholander, 1958). On the other hand, the gas-gland cells might not accept oxygen from the blood unless the tension was higher than that in the swimbladder. This aspect must be left for future experiments: here we may simply remark on the significance of long capillaries for the efficient exchange of gases in the retia, particularly in those of deep-sea fishes. Regardless of the attainment of high pressures, a deep-sea fish must have well-developed retia in order to prevent the loss of gases from the swimbladder. Using his equations and reasonable values for the various constants, Scholander (1958, p. 9) calculated '. . . that the exchange through the rete in a deep-sea eel is so great that if the blood in swimbladder has an oxygen tension of two hundred atmospheres it will leave the bladder with an oxygen tension only a few millimetres higher than in the arterial blood'.

In proportion to the size of the swimbladder, bathypelagic teleosts have large retia mirabilia, the relative development of these systems being greater than those of shallow water species (Marshall, 1950, 1954; Jones and Marshall, 1953). This difference may be given rough quantitative expression by obtaining values of the ratio $l < b/r$ for species from the two types of environment (l and b being the lengths of the major and minor axes of the sac (which approaches an ellipsoid in form) and r the length of the retial capillaries).

Values of this ratio are given in Table 4 (p. 74) for various species of deep- and shallow-water fishes. Drawings of the swimbladders of some of the latter species may be found in Text-fig. 36.

The first six species in the shallow-sea group are epipelagic fishes. It will be seen that the ratios in these species are far higher than the figures obtained for the deep-sea species. But as regards a counter-current exchange-system it is the absolute rather than the relative length of the retial capillaries that is significant. However, apart from *Pollichthys*, *Vinciguerria*, *Argyropelecus* and *Astronesthes* among the deep-sea group and *Hyporhamphus* from the epipelagic species, the retia of the bathypelagic species are longer (some much longer) than those in the surface-swimming species. And there is another factor to be considered, the diameter of the capillaries, for the smaller this is the greater the efficiency of gaseous exchange. Two of the exceptions among the deep-sea group have relatively small capillaries, which measured $7-8\,\mu$ in diameter in *Argyropelecus* and *Vinciguerria*. (There are no data for the other two.) In the epipelagic species the capillaries are $10\,\mu$ or more in diameter.

Table 4 also reveals that the ratios and retial dimensions of *Gadus minutus* and *Capros aper* are close to those of the bathypelagic species: this is not surprising in view of the depth-range of these two fishes.

Considering only the deep-sea fishes, it would be reasonable to expect that the deeper the living space the longer would be the retia. In Table 4 it will be seen that the retia of *Stephanoberyx monae* and *Melamphaes megalops* are much longer than those of the other deep-sea fishes. Now the first species may well be demersal rather than pelagic in habit and it has a depth-range extending down to 2295 m. (Grey, 1956). Norman's (1929, 1930) data for *Melamphaes megalops* suggests that this fish tends to be concentrated well below the 500-m. level. The populations of the other species tend to be centred above this depth. Even more striking instances of this correlation between the retial span and depth can be found if abyssal fishes are also considered. But this will best be left until the final section of this report.

The gas-gland

In parallel with their retia, the gas-glands of bathypelagic teleosts are relatively large compared with those of shallow-water species. Some attention has already been drawn to this (Marshall, 1950, 1954; Jones and Marshall, 1953). Here a closer comparison will be made between various epipelagic
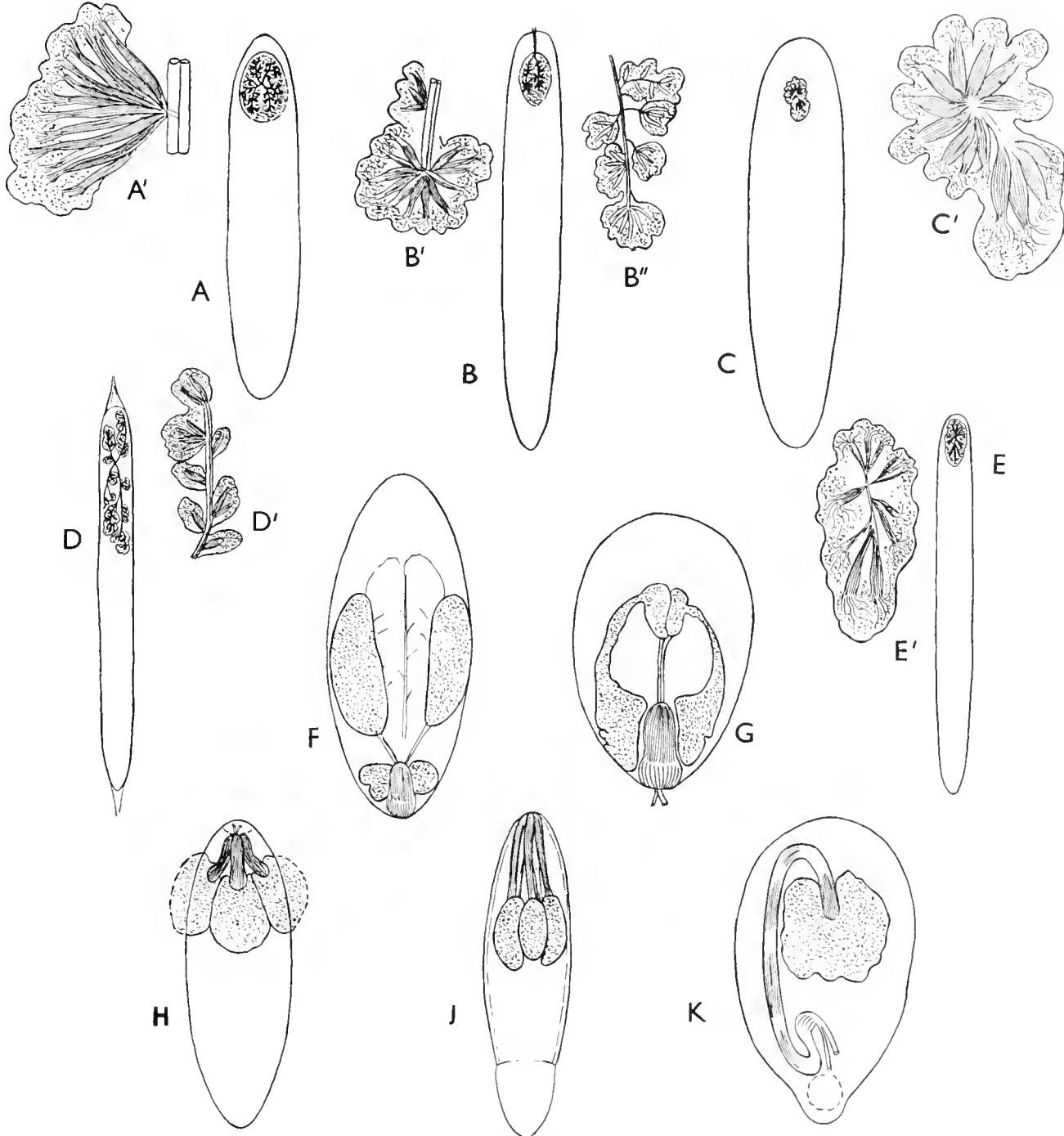
Text-fig. 36. Swimbladders of some epipelagic and bathypelagic fishes, showing the relative developments of the retia mirabilia and gas-glands. Epipelagic species: (A, A') *Cypsilurus cyanopterus*; (B, B', B'') *Danichthys rondeletii*; (C, C') *Exocoetus volitans*; (D, D') *Petalichthys capensis*; (E, E') *Hyporhamphus* sp. Bathypelagic species: (F) *Vinciguerria attenuata*; (G) *Argyropelecus aculeatus*; (H) *Myctophum punctatum*; (J) *Chiasmodon niger*; (K) *Melamphaes megalops*. Gas-gland dotted; retia, with striations along the major axes. In A', B', B'', C', D' and E' part or the whole of the gas-secreting complex is shown enlarged. (A, × 0·38; A', × 10; B, × 0·6; B', × 5; B'', 2·5; C, × 1; C', × 5; D, × ½; D', × 5; E, × 1; E', × 4; F, × 10; G, × 10; H, × 3·8; J, × 6; K, × 5.)

Table 4. *Swimbladder dimensions and retial lengths of some bathypelagic and shallow-water teleosts*

Species	Length of major axis l (mm.)	Length of minor axis b (mm.)	Length of retia r (mm.)	$\dfrac{lb}{r}$ (ca)
Deep-sea				
Gonostoma denudatum	16·0	2·0	2·5	13
Pollichthys mauli	5·0	2·0	1·2	8
Bonapartia pedaliota	10·0	5·0	3·6	14
Vinciguerria attenuata	8·5	2·75	0·8	29
Argyropelecus aculeatus	8·5	4·5	1·5	26
Polyipnus laternatus	6·0	3·5	3·0	7
Astronesthes niger	5·5	2·5	1·5	9
Myctophum punctatum	12·0	4·5	2·2	25
Diaphus rafinesquei	20·0	6·0	2·5	48
Lampanyctus güntheri	9·5	2·0	2·8	7
Melamphaes megalops	8·5	5·0	12·0	4
Stephanoberyx monae	16·0	8·0	8·0	16
Chiasmodon niger	16·0	3·0	3·5	14
Shallow sea				
Cypsilurus cyanopterus	140·0	20·0	1·5	1870
Danichthys rondeletii	90·0	10·0	1·25	720
Exocoetus volitans	58·0	6·0	1·75	200
Petalichthys capensis	107·0	6·0	1·0	640
Hyporhamphus sp.	60·0	5·0	2·5	120
Scombresox saurus	105·0	6·0	1·25	500
Gadus minutus	38·0	6·0	3·0	75
Capros aper	23·0	6·0	2·5	55

and bathypelagic species. The extent of the gas-glands of some of these fishes can be seen in Text-fig. 36.

While these drawings give a ready impression of the relatively large expanse of the glands in deep-sea species, a more meaningful comparison may be made by estimating the ratio of the surface-area of the gas-gland to the volume of the swimbladder. Measurements were made only on fishes showing good expansion of the gland and swimbladder, the results being given in Table 5. Before considering these figures it should be remembered that the comparison of gas-glands in terms of surface-area is not entirely appropriate, since some are more than one cell in thickness. But as the glands of the three flying fish appear to be no more than one cell thick, this will not bias the figures in favour of the deep-sea species. Of these, *Vinciguerria attenuata* and probably the two *Astronesthes*, have single layer gas-glands, while those of *Argyropelecus* and the three lantern fishes are multi-layered.

The proportionately greater glandular surface in the bathypelagic species will be immediately obvious. The contrast is as great as that between the two environments. The flying fishes spend most of their life not far below the surface, while the populations of the deep-sea species are centred at various levels between 200 and 1000 m.

The significance of these differences may be appreciated by comparing the flying-fish, *Cypsilurus cyanopterus*, with the lantern fish, *Myctophum punctatum*. A 600-g. *Cypsilurus* will have a swimbladder volume of about 30 ml., while the corresponding figure for a 5-g. *Myctophum* will be 0·25 ml. Assume that the flying fish and lantern fish live at mean pressures of 1·5 and 30 atmospheres respectively. Considering the swimbladders only during the steady state, when the gas lost by diffusion is being made up by secretion, we may further assume that the flying-fish loses 5 per cent of the contained gases during the course of a day. The same percentage may be taken for the lantern fish

for the time it spends at its daytime level (say, 12 hr.). To make good this loss, the flying-fish must secrete 1·5 ml. gas at a pressure of 1·5 atmospheres. The lantern fish must produce 0·0125 ml. at 30 atmospheres or 0·25 ml. at 1·5 atmospheres. Thus, while the volume of the flying-fish swimbladder is 120 times that of the lantern fish, the relative amounts of gas required to restore a gradual loss of buoyancy differ by no more than a factor of 6.

Table 5. *Relative development of the gas-gland in some epipelagic and bathypelagic fishes*

Species	Standard length (mm.)	Surface-area of gas-gland (mm.²):volume of swimbladder (mm.³)
Epipelagic		
Cypsilurus cyanopterus	290·0	1/120
Danichthys rondeletii	214·0	1/120
Exocoetus volitans	159·0	1/160
Hyporhamphus sp.	112·0	1/25
Bathypelagic		
Astronesthes niger	41·0	1/4
A. similis	104·0	1/6
Vinciguerria attenuata	43·5	1/7
Argyropelecus aculeatus	23·0	1/7
Benthosema suborbitale	24·0	1/2
Lampanyctus güntheri	53·0	1/3
Myctophum punctatum	71·0	1/5
Melamphaes megalops	56·0	1/16
Chiasmodon niger	104·0	1/4

However, in estimating the figures in Table 5, it was found that a *Cypsilurus* of the above weight has a gas-gland with a surface-area of 25 mm.², while the figure for the lantern fish is about 20 mm.² Furthermore, the lantern fish has a gas-gland consisting of many layers of cells, whereas that of the flying fish is probably single-layered. This would suggest that the lantern fish is readily able to make up the loss of gas. But, unlike the flying-fish, the lantern fish undertakes extensive vertical migrations. Towards sunset it will climb several hundred metres towards the surface-layers, and after spending the hours of darkness near the surface, will then dive to its daytime depth. In considering the relative development of the gas-gland, it is clear that vertical migrations must also be taken into account. This will best be dealt with at a later stage (p. 89). Here we may turn to the fine structure of the gas-glands.

In shallow-water fishes there is considerable variability in the fine structure of the gas-glands (Woodland, 1911*a*; Fänge, 1953) and this is also true of deep-sea fishes. However, three main groups may be recognized (see Text-fig. 37).

(1) Gas-glands consisting mostly of giant cells. Capillaries partly intracellular. *Vinciguerria* and *Sternoptyx*. In the first genus the cells of the expanded gas-gland measure from 100 to 150*μ* in length. Nusbaum-Hilarowicz (1920) gives the dimensions of the cells of *Sternoptyx* as 50–95*μ*. In *Vinciguerria* the extent of the intracellular capillaries is considerably greater than that of the intercellular elements, but the reverse seems to be true of *Sternoptyx*.

(2) Gas-glands consisting mostly of medium-sized cells. Capillaries intercellular. *Cyclothone*, 20–50*μ*; *Maurolicus*, 20–40*μ*; *Argyropelecus*, 25–50*μ*; *Polyipnus*, 25–50*μ*.

(3) Gas-glands with small cells. Capillaries intercellular. *Myctophum punctatum*, 15–20*μ*; *Diaphus dofleini*, 10–15*μ*; *Opisthoproctus soleatus*, 15–25*μ*.

Giant cells are also found in the gas-glands of shallow-water fishes, such as *Carapus*, *Perca* and

Zeus. In reviewing the available information, Fänge (1953) suggests that such cells may be quite common among euphysoclists. But the two genera in the first group of deep-sea fishes appear to be unique in having glands that are largely composed of giant cells. In *Vinciguerria* these cells may be as much as 100μ in depth, a striking contrast to the 10–15μ cells of the gas-gland of *Diaphus dofleini*, which are disposed in several layers to a depth of about 200μ. The gas-gland of *Vinciguerria* is also remarkable in two other ways, the first being that the greater part of the contact between the giant
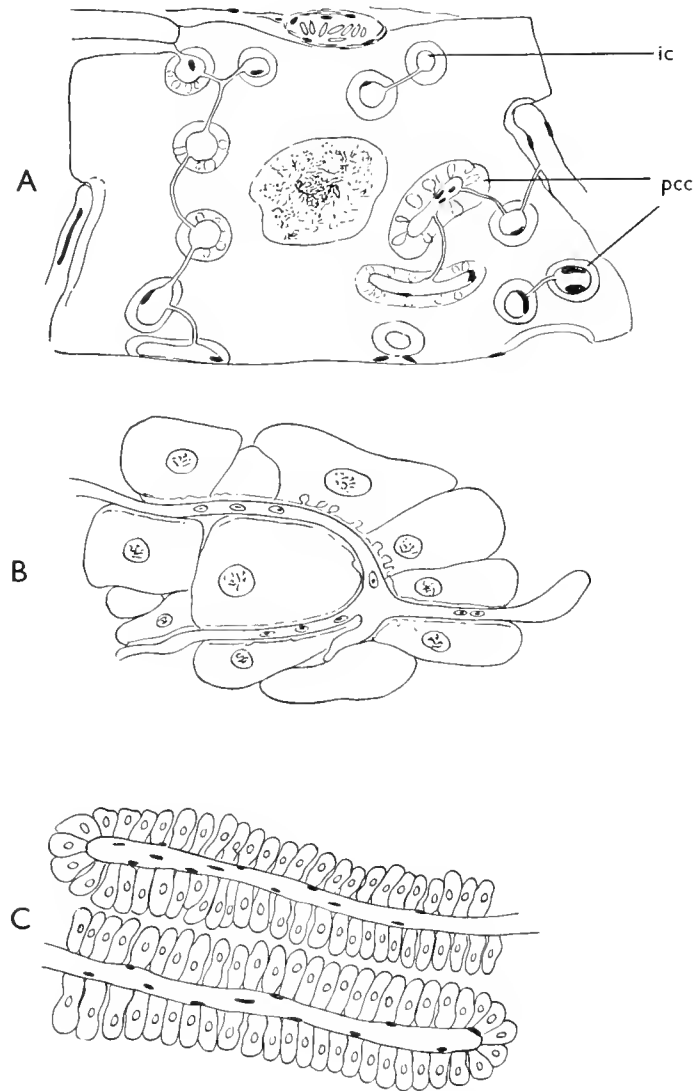
Text-fig. 37. Three types of gas-glands in bathypelagic fishes; (A) consisting mostly of giant cells (*Vinciguerria*), with intracellular capillaries; (B) with medium-sized cells (*Polyipnus*), and (C) with small cells (Myctophidae). The base of the cell of *Vinciguerria* is 170μ in length, while the cell of *Polyipnus* fitting into the U-bend of a capillary is about 50μ wide. The cells of *Myctophum* are from 10 to 17μ in length along their longer axes. *ic*, intracellular capillary; *pcc*, pericapillary cytoplasm.

cells and the capillaries supplying them is within the cytoplasm. Secondly, these intracellular capillaries connect with one another through fine canals in the cytoplasm, the lumen of the canals being little more than 1μ across, too fine to admit the elliptical red blood corpuscles, which are about 6–8μ long and 2–3μ wide.

A number of workers (see Fänge, 1953) have observed that the cytoplasm around the capillaries stains differently from the remaining cell contents. I have also seen this in the gas-glands of *Argyropelecus, Polyipnus, Vinciguerria, Maurolicus, Cyclothone* and *Opisthoproctus*. After staining with

haemalum and eosin, the pericapillary cytoplasm has a hyaline, homogeneous appearance, which contrasts with the lilac or salmon-pink colour of the other cell contents. The hyaline border varies from 2 to 6μ in thickness.

In his plates of the gas-gland of *Sternoptyx*, Nusbaum-Hilarowicz (1920) shows the pericapillary borders to have a striated appearance, and this has also been reported in other fishes by Vincent and Barnes (1896) and by Bykowski and Nusbaum (1904). Like Fänge (1953), I was unable to detect this, but the sections of the giant cells of *Vinciguerria* did reveal that the interface between the blood-system and the cytoplasm can be the site of intense activity. The borders look as though they are breaking down to form small vacuoles (Pl. II, fig. 3) and this process seemed also to be taking place along the intercapillary canals in the cytoplasm. In sections of the gas-gland of *Polyipnus laternatus* the pericapillary border almost had a striated appearance, but closer examination showed the striation to be a series of elongated 'vacuoles' aligned normally to the bore of the capillaries.

These cytoplasmic inclusions cannot be gas-bubbles as they have a different optical appearance, and in *Vinciguerria*, the hyaline blobs that appear along the capillaries look very like the vacuoles that are lying free in the cytoplasm. It may also be significant that the vacuoles are generally larger near the interface between the gland cells and the swimbladder cavity.

In a series of papers, Scholander and his colleagues (Scholander and van Dam, 1954; Scholander, 1954, 1956; Sundnes, Enns and Scholander, 1958) have argued that the Root effect (the release of oxygen from oxy-haemoglobin by a lowering of the pH of the blood) plays little part in the secretion of this gas against the high oxygen pressures that exist in the swimbladders of deep-sea fishes. (By using marked oxygen (O^{18}) Scholander, van Dam and Enns (1956) showed that the gas must come from the water surrounding the fish (cod) and be transported as oxy-haemoglobin from the gills to the swimbladder).

In particular, if the lower limit of the blood pH is taken as 6·5, the Root effect is almost non-existent in deep-sea fishes, such as the long-nosed eel (*Synaphobranchus-pinnatus*), the blue hake (*Antimora violacea*) and the round-nosed ratfish (*Coryphaenoides rupestris*), but is well marked in shallower-water species like the tautog (*Tautoga onitis*). (Scholander and van Dam (1954) determined the oxygen dissociation of the blood at oxygen-tensions from 0·2 to 140 atmospheres and at acidities down to pH 5·6.) Thus in deep-sea fishes the oxygen seems not to be liberated directly from the blood, but to be actively secreted by the gas-gland cells. Furthermore, even in the shallow water toadfish (*Opsanus tau*), Wittenburg (1958) has shown (in a very neat way) that the gas-gland cells are able to transport oxygen from the blood plasma into the swimbladder. After supplying the fish with carbon monoxide in (presumably) sufficient quantities to immobilize the haemoglobin, oxygen was still secreted into the swimbladder. Wittenburg suggested that this active transport of gas is by way of an iron-haem protein.

Perhaps the foregoing observations of the gas-gland cells of *Vinciguerria* also support this idea. Perhaps there are three main phases in the formation of the gas bubbles that are eventually released into the swimbladder. The first consists of an intense interaction between the blood and the peri-capillary cytoplasm, when vacuoles are formed. Fänge (1953) has shown this part of the cytoplasm to be devoid of glycogen, while acid-phosphatase activity seems to be concentrated around the peripheral zones of the gland cells. The second phase would be the growth of those vacuoles and their transport to the interface between the cell and the lumen of the swimbladder. Some of the energy for this process would be provided by the breakdown of glycogen. The vacuoles may discharge their contents into the mucous fluid covering the gas-gland, after which gas bubbles are formed (third phase) eventually bursting to release their contents (mainly oxygen) into the swimbladder cavity. (Gas-bubbles have never been observed within the gland cells.) The function of the vacuoles would

be to supply 'high tension' gas-nuclei around which the bubbles could form. However, due to surface-tension, the gas-pressure within a bubble is inversely related to the diameter of the bubble, which means that considerable pressures will be required for its growth. But in the foam found in lung-alveoli, Pattle (1958) discovered that the surface-tension of the bubbles was much reduced by a surrounding layer of insoluble protein. Perhaps the foam covering the gas-gland has somewhat similar properties.

In conclusion, it must be acknowledged that little is known of gas-secretion by the swimbladder, particularly in deep-sea fishes. As Scholander (1956, p. 523) has written: ' In spite of all the information available regarding the function of the gas-gland in fishes, one may safely say that none of the three cardinal feats of the gland can as yet be explained: namely, the production of 100–200 atmospheres of oxygen, of 10–20 atmospheres of nitrogen and of 0·1–0·2 atmospheres of argon.' In the endeavour to solve these problems the giant cell gas-gland of *Vinciguerria* should provide excellent experimental material, particularly for histochemical studies.

THE RESORBENT PART OF THE SWIMBLADDER

We have already seen that the swimbladder volume of a marine teleost must be kept near or equal to some 5 per cent of the body volume. There is evidence that teleost fishes have a certain latitude of movement above a level of neutral buoyancy (Scholander, Claff, Teng and Walters, 1951; Jones, 1952), but beyond this range the fish will tend to be 'ballooned' out of control as the volume of its swimbladder (and hence its own volume) increases. Apart from the dangers of injury, an upward migration involving a threefold increase in the volume of the swimbladder means that the fish must exert (by compensatory movements) an upward force equal to about 10 per cent of its weight in air in order to make 'downwards headway' (Denton and Marshall, 1958).

During a migration towards the surface, a teleost with a closed swimbladder must reduce the volume of the sac to a manageable, just buoyant, level by loss of the contained gases to the blood. This diffusion takes place through special resorbent surfaces with a rich supply of capillaries, some account of which has been given in the earlier descriptive section (pp. 7–50). These findings can now be summarized and discussed. Other aspects will also be considered in a later section on vertical migrations.

Order *Isospondyli*, Suborder Stomiatoidea

In this group there is a close association between the resorbent system and the gas-gland, for the venous return from the capillaries is generally by way of veins running from the gland to the rete mirabile. These veins may return from the gland (*Astronesthes niger*, *Vinciguerria* and *Maurolicus*), or run along the inner edge of the gland (*Pollichthys*). *Argyropelecus* also has periglandular veins but these may also pass through the gland. (With the material available it was not possible to make a close study of these venous channels.)

The arterial capillaries of the resorbent surface are formed from a branch of the retial artery which leaves this vessel just before it flows into the rete, to run forward alongside the latter. On reaching the resorbent area, it breaks up into arterioles and capillaries, which together with the venous elements, form the resorbent complex.

Since the venous blood from this complex eventually flows through the rete mirabile, a bipolar retial system would appear to be essential. To supply the venous part of a resorbent area a unipolar rete would have to give off hundreds of separate venous capillaries, which might then have to run for considerable distances before meeting their arterial counterparts (see, for instance, *Vinciguerria*, *Maurolicus* and *Astronesthes niger*). Such an arrangement might well be functionally unbalanced

with the arterial system, particularly in fishes that make upward vertical migrations. To keep the swimbladder from over-inflation the rate of gas-removal should be high: hence the need to remove venous blood from the capillary system as quickly as possible (see also pp. 92–94).

The resorbent circulation of the stomiatoid swimbladder would appear to be unique among deep-sea fishes (perhaps also among teleosts in general). It presumably functions as follows: During gas-resorption, contraction of the arterioles forming the retial capillaries will close down the flow of arterial blood through the rete (Fänge (1953) has shown how such contraction can lead to capillary closure). As the retial artery is still open blood can only flow down the arterial branch supplying the resorbent area. Blood returning from the system will be free to flow through the rete, since the venous capillaries will be fully open (presumably they have extra room for expansion owing to the virtual closing of their arterial counterparts). During gas-secretion both sets of retial capillaries will be open and the gas-gland fully expanded. Arterial blood will now flow from the retial artery into the dilated arterioles (and so through the rete) rather than down the by-pass vessel into the resorbent system. Furthermore, when the gas-gland is expanded, the resorbent system is contracted (Fänge, 1953) and this may well lead to a stoppage of the resorbent circulation.

Just how this antagonistic action of the secretory and resorbent mucosa is brought about in the stomiatoids has yet to be determined. In euphysoclist teleosts, the action is perfectly clear (see p. 81 of this section). However, the smooth muscles of the swimbladder wall are likely to be involved. (In *Argyropelecus* and *Polyipnus* the muscle layer is close to the inner epithelium.) The disposition of the fibres may be such that those controlling the expansion of the capillary network are contracted during resorption, while those around the gas-gland are relaxed. The opposite would occur during gas-secretion. An extreme instance of this antagonism may be seen in Text-fig. 32 of the swimbladder of *Vinciguerria*.

Dissections made of two specimens of *Argyropelecus aculeatus* show the swimbladder as it probably appears during the resorptive and secretory phases. Considering only the former condition, the relatively large expanse of the capillary layer and the bunching up of the gas-gland is particularly striking (Text-fig. 38).

As already indicated, the capillary circulation of stomiatoids is unique in that the venous return-flow is through the rete mirabile. In the groups now to be considered the secretory part of the swimbladder is perfectly distinct from the resorbent part, this having a separate venous system (which usually runs into the hepatic or cardinal veins). Teleosts with such a swimbladder are called euphysoclists and are to be distinguished from paraphysoclists, those in which the two parts are not so sharply delimited (Rauther, 1922).

SALMONOIDEA (deep-sea). In a recent revision of the argentinine fishes (genera *Argentina* and *Glossanodon*), Cohen (1958) has shown that the swimbladder has two distinct parts, comprising an anterior, thick-walled, cylindrical chamber and a posterior, thin-walled diverticulum. From Fänge's (1958) observations and my own, it is clear that the anterior chamber contains the gas-gland and the micro-retia. Cohen described the posterior diverticulum as having a vessel from the distal end that seemed to drain into the renal portal system (or is this the dorsal aorta?), while a vein from the front of the down-turned part leads to the hepatic portal vein. In a specimen of *Argentina sphyraena* (standard length 170 mm.), I found a well-marked posterior diverticulum in which the down-turned part, that runs forward beneath the thick-walled chamber, measured 13 mm. in length. The inner epithelium of this part was thrown into folds and contained a capillary network. There is thus good indication that the diverticulum is the resorbent part of the swimbladder. I also found a thin-walled posterior chamber in *Microstoma microstoma*, but this had no down-turned antrorse section. *Nansenia* may also have such a structure (the individual I examined was not well-preserved).

In *Winteria* and *Opisthoproctus* the swimbladder does not appear to be differentiated into two sharply demarcated sections. The micro-retia and gas-gland are certainly found in the anterior part of the sac, but behind this the walls seem just as thick. Perhaps the capillary system is found in the rear part of the sac, but I was unable to ascertain this in the material at my disposal.
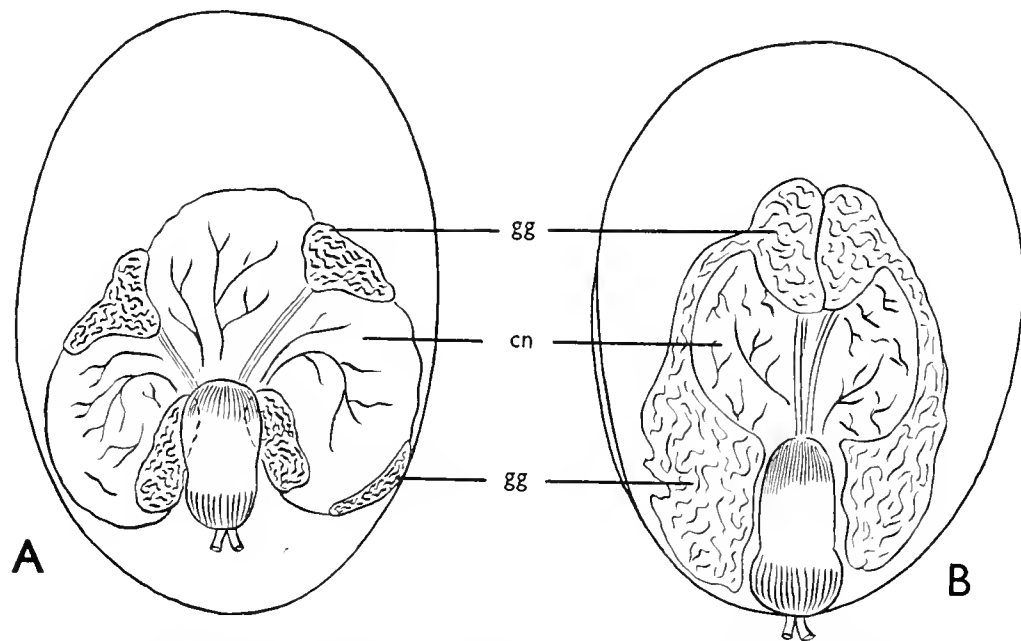
Text-fig. 38. Swimbladder of *Argyropelecus aculeatus*, (A) with the resorbent capillary network expanded and the gas-glands contracted, (B) with the capillary network relaxed and the gas-glands expanded. *cn*, capillary network; *gg*, gas-gland.

Order *Iniomi*, Suborder Myctophoidea

MYCTOPHIDAE. The resorbent surface of the lantern fish swimbladder is an 'oval' like that found in various gadoid, macrourid and spiny-finned fishes. It is a thin-walled circular part of the swimbladder and is surrounded by radial and circular smooth muscle fibres, having an antagonistic action. When the radial fibres contract (the circular ones being relaxed), the oval with its rich supply of capillaries is stretched and exposed to the gases in the swimbladder. The circular muscles act as a sphincter. As they contract the thick-walled parts of the swimbladder wall surrounding the oval are drawn towards its centre, eventually coming together. As the oval shuts, its walls are thrown into ridges and folds, and at the end of the process it looks like a wrinkled projection on the face of the sac.

In most of the myctophids I dissected, the oval had this appearance. It was fairly well expanded in two specimens of *Myctophum punctatum* and one of *Diaphus dofleini*, and half-open in a specimen of *D. rafinesquei* and of *Lampanyctus guentheri*. It has already been suggested that the structure Rauther (1922) described in *Diaphus rafinesquei* as the praevesica is actually an oval, and the same is presumably true of the conical projection found at the front end of the swimbladder of *Lampadena chavesi* (see pp. 38–39).

A longitudinal section of a closed oval in *Myctophum punctatum* is shown in Pl. III. At high magnifications the circular and radial muscles could be seen, the former having a 'bunched-up' appearance. The inner epithelium, close to which lies the capillary network, is thrown into folds, while the tissues in the walls have relaxed during the closure. No doubt this accommodation is made possible by the semi-gelatinous nature of the submucosa, although in the oval of the perch (*Perca fluviatilis*) Saupe (1939) found the gelatinous and fibrous components to be much reduced.

The myctophid oval lies at the anterior end of the swimbladder close to the retia mirabilia (see

Text-figs. 15–23). Its arterial supply usually comes from a branch or branches of the retial artery, while the venous return is through a vessel draining into the cardinal vein.

Order *Miripinnati*

In these teleosts the swimbladder is only functional during the larval phase (Bertelsen and Marshall, 1956). As in certain percomorph fishes, the anterior, thick-walled secretory part is sharply distinct from the posterior thin-walled section, but there is no intervening diaphragm. Although it has not been closely examined, there can be little doubt that the thin-walled part is concerned with gas-resorption.

Order *Berycomorphi*, Suborder Anoplogastroidea

Both the Melamphaidae and *Stephanoberyx* have a typical 'oval' which is set on the roof of the swim-bladder near its posterior end. A drawing of the almost closed oval of a *Melamphaes megalops* is shown in Text-fig. 27. In the specimen of *M. unicornis* (Text-fig. 28) examined, the oval, from which a large vessel drains into the cardinal vein, was completely closed. The oval of the *Stephanoberyx monae* was in much the same condition as that of *Melamphaes megalops*.

Order *Percomorphi*

CHIASMODONTIDAE. *Chiasmodon niger*. In this species a diaphragm divides the anterior gas-secreting chamber from the posterior resorbent chamber. Such a partition is found in the Solenichthyes, Thoracostei, certain Percomorphi and Scleroparei (Fänge, 1953 and personal observation) and is probably quite common in zeomorph fishes (a diaphragm is found in *Zeus faber*). As Fänge (1945, 1953) has shown, the movements of this diaphragm are controlled by the antagonistic action of the secretory and resorbent parts. During gas-production the muscle fibres of the secretory part relax, while those of the resorbent mucosa are contracted. The antagonism reverses during gas-resorption. Considering first the latter, the contraction of the muscles in the secretory chamber pulls the diaphragm to the forward end of the swimbladder, while the relaxation of the resorbent layer ensures that the capillary layer is expanded and fully exposed to the gases. During secretion the diaphragm moves to the posterior end of the sac and now the gland is fully expanded.

The swimbladders of the three *Chiasmodon* examined each show different phases of this process (Text-fig. 29). In the 104-mm. fish the gland is bunched up and its chamber occupies no more than one-fifth of the total length of the swimbladder. This fraction is rather more than a half in the 49-mm. fish, while in the third fish it is a quarter. Having regard to the previous paragraph, it is evident the swimbladder of the first and third fishes show the disposition of the tissues during resorption and secretion respectively.

BATHYPELAGIC FISHES WITHOUT A SWIMBLADDER

Summarizing the earlier descriptive section, the following groups either lack a swimbladder, or it is regressed in the adult phase:

Order *Isospondyli*. Suborder Stomiatoidea: GONOSTOMATIDAE, *Cyclothone* spp., *Gonostoma elongatum*, *G. bathyphilum*; ASTRONESTHIDAE, (in *Diplolychnus mononema*, *Borostomias antarcticus*, *Astronesthes gemmifer*, the swimbladder seems to regress during adult life); STOMIATIDAE; MELANOSTOMIATIDAE; CHAULIODONTIDAE; IDIACANTHIDAE; MALACOSTEIDAE.

Suborder Salmonoidea: BATHYLAGIDAE.

Suborder Clupeoidea: ALEPOCEPHALIDAE (many of these fishes appear to be benthic in habit); SEARSIDAE.

Order *Iniomi*. Suborder Alepisauroidea. Suborder Myctophoidea: SCOPELOSAURIDAE; MYCTO-
PHIDAE: while most species have a swimbladder, the following species lack this organ: *Lampanyctus
braueri*, *Ctenobranchus nigro-ocellatus*, *Gonichthys coccoi*, *Diaphus coeruleus*. In *Electrona antarctica*,
the swim bladder regresses during the adult phase and as already mentioned (p. 65), the swim-
bladders of *Lampanyctus leucopsarus* and *Diaphus theta* are reduced and invested with fat.

Order *Cetunculi*, Order *Miripinnati*, Order *Giganturoidea*, Order *Lyomeri*. Order *Allotriognathi*:
Stylophorus chordatus. Order *Berycomorphi*, Suborder Anoplogastroidea: *Anoplogaster longidens*,
Melamphaes mizolepis. Order *Percomorphi*, CHIASMODONTIDAE: *Pseudoscopelus scriptus*, *Dysalotus
alcocki*. Order *Pediculati*, Suborder Ceratioidea.

VERTICAL DISTRIBUTION AND THE SWIMBLADDER

In his 'Challenger' Report, Günther (1887, p. xxxiii) has written: 'I formerly assumed that the fishes
of the open sea were living either near to the surface or at the bottom, but I think now that Mr Murray
is right in supposing that certain fishes live habitually in intermediate strata, without ever coming to
the surface or descending to the bottom.' The biologists of the 'Valdivia' Expedition (1898–9) were
the first, however, to give close consideration to the fact that deep-sea fishes live at different levels in
the ocean. After distinguishing between benthic and bathypelagic species, Brauer (1906) proceeded
to discuss this problem and the difficulties involved with the use of open-nets. But the expedition
did fish some closing-nets and Brauer gave examples of species taken with this gear (e.g. St. 120,
Cyclothone microdon, 1500–900 m.; St. 227, *Sternoptyx diaphana*, 800–600 m.; St. 229, *Lampanyctus
nigrescens*, 1000–800 m.). The Deutsche Südpolar Expedition (1901–3) used open vertical and hori-
zontal nets, and some details are given of the apparent vertical distributions of the deep-sea fishes that
were taken (Pappenheim, 1914).

Since these earlier expeditions, our knowledge of the depth distribution of bathypelagic fishes has
been largely due to the 'Michael Sars' Expedition in 1910 (Murray and Hjort, 1912); the Danish
Oceanographic Expeditions in the Mediterranean and adjacent Atlantic waters during 1908–10
(Jespersen, 1915; Tåning, 1918 and Jespersen and Tåning, 1926); the Discovery Investigations
(Norman, 1929, 1930); the Dana Expeditions (Regan and Trewavas, 1929, 1930; Bertin, 1934, 1937;
Ege, 1934, 1948, 1953; Bruun, 1937, Bertelsen, 1951 and Bertelsen and Marshall, 1956) and the
Bermuda Oceanographic Expeditions (Beebe, 1937). From these and other publications, Grey (1956)
has compiled a valuable and detailed survey of the bathypelagic and benthic fishes found below
a depth of 2000 m. A more general appreciation of vertical distribution may be found in Marshall (1954).

Besides tangible evidence from the nets, underwater observations are now beginning to play their
part. Since Beebe's (1934) dives in a bathysphere, a number of observers have been down in bathy-
scaphes. To take but one account (Pérès, 1958), it is clear that an experienced observer can both
enlarge and corroborate present knowledge. During three dives off Cap Sicié, Pérès found that the
schools of lantern fishes not only occurred in a mid-water layer (mainly from 400 to 700 m.), but were
also clustered close to the bottom (about 10 m. above 1500 m.). He also saw that *Argyropelecus
hemigymnus* is found between 250 and 600 m. (with a maximum at 350–400 m.), which is a striking
confirmation of Jespersen's (1915) estimates from open-nets.

These findings, so far as they concern the fishes dealt with in this report, may now be summarized:

A. *Fishes with centres of concentration between depths of about 200 and 1000 m.*

Reference to the papers cited earlier will show that any species may have a considerable vertical
range about its centre of concentration. And, apart from diurnal migrations, the main depths of

occurrence may vary in space and time. Species living in very transparent waters live further down than their relatives in less clear waters (comparison of Beebe's (1937) and Grey's (1955) data with those obtained in other parts of the Atlantic (Murray and Hjort, 1912) reveals this). Furthermore, the higher the latitude the less the depth of maximum concentration (Murray and Hjort, 1912). There may also be seasonal changes, species tending to live nearer the surface during the winter months (Jespersen and Tåning (1926), Tåning (1918)).

Order *Isospondyli*. Suborder Stomiatoidea. Apart from those listed in section B, most stomiatoids seem to belong here. Suborder Salmonoidea: *Opisthoproctus*, *Winteria*, BATHYLAGIDAE. Apart from *Bathylagus argyrogaster*, which was taken mainly above 500 m., the commoner species taken during Discovery Investigations appear to be concentrated between 500 and 1000 m. (Norman, 1930).

Order *Iniomi*. Most alepisauroids (Marshall, 1955) and Myctophidae.

Order *Giganturoidea*, Regan, 1925.

Order *Allotriognathi*, *Stylophorus chordatus* (Bruun *et al*. 1956).

Order *Berycomorphi*: MELAMPHAIDAE. The commoner species taken in Discovery nets (Norman, 1929, 1930) appear to come from depths between 500 and 1000 m.

B. *Fishes with centres of concentration between depths of about* 1000 *and* 4000 *m*.

Order *Isospondyli*. Suborder Stomiatoidea: GONOSTOMATIDAE, *Cyclothone microdon*, *C. livida*, *C. acclinidens*, *C. obscura*, *Gonostoma bathyphilum*.

Order *Lyomeri*. The centre of distribution of *Eurypharynx pelecanoides* seems to lie between 1400 and 2800 m. (Grey, 1956).

Order *Apodes*. Certain of the deep-sea eels such as *Cyema atrum*, *Serrivomer parabeani* and *Avocettina infans* appear to be commoner at these deeper levels (Grey, 1956).

Order *Berycomorphi*: *Melamphaes nigrescens* (Grey, 1956) and possibly *M. cristiceps* (Norman, 1929, 1930) occur below 1000 m.

Order *Pediculati*: Suborder Ceratioidea. Metamorphosing, adolescent and adult deep-sea angler fishes are mainly to be found at or below a depth of 1500 m. (Bertelsen, 1951).

By referring to the descriptive part of this report, it will be clear that the populations of bathypelagic fishes with fully developed gas-filled swimbladders are centred in the upper reaches (200–1000 m.) of the deep-sea. The main groups are the Gonostomatidae (most species), Sternoptychidae (hatchet fishes), *Astronesthes* spp. Myctophidae, and Melamphaidae (most species). While numerous species from these levels lack a swimbladder [the Melanostomiatidae, Stomiatidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Bathylagidae, Alepisauroidea and Giganturoidea are the main groups (but see also the summary on p. 81–82)], this condition is universal in the fishes centred between depths of 1000 and 4000 m.

Hydrostatic pressure increases by one atmosphere for each 10 m. of depth and the average depth of the ocean is about 4000 m. It might thus be supposed that the limitation imposed on the development of a gas-filled hydrostatic organ is simply related to the pressure factor. Clearly, the aspects to be considered concern the compressibility of gases and the amounts of energy and gas required to keep the swimbladder inflated at the appropriate volume against high hydrostatic pressures.

COMPRESSIBILITY OF GASES

The swimbladder gases of deep-sea fishes consist largely of oxygen (Scholander and Van Dam, 1953; Kanwisher and Ebeling, 1957) and this gas alone will be considered.[1] At normal temperature and pressure the density of oxygen is 1·429 g./l., which value is about one seven-hundredth of the density of sea-water. In other words, at a depth of 7200 m., the density of oxygen is equal to that of seawater, and the gas would thus have lost its positively buoyant properties.

A fish having 95 g. of fat-free tissue, with a density of 1·076 (taking Taylor's (1921) estimate) and a 5-ml. swimbladder will have a density of about 1·07, which is well above the value for seawater (1·028) at this depth. Clearly a gas-filled swimbladder would be virtually useless. However, we shall see later that abyssobenthic fishes with well-developed swimbladders may range as deeply as 5000 m. At such a level the density of oxygen is about 0·7. Thus to achieve neutral buoyancy, either the volume of the swimbladder must be considerably increased or the density of the tissues be reduced. There is no evidence of the first desideratum being met, but there is good indication of a general lightening of the tissues (see p. 96).

ENERGY REQUIREMENTS OF THE SWIMBLADDER

The combined partial pressures of the gases dissolved in seawater at any depth total no more than one atmosphere. The oxygen tension is thus about one-fifth of an atmosphere, yet the partial pressure of this gas in the swimbladder may be 200 atmospheres or more (Scholander, 1954). Thus, between the uptake of oxygen by the blood circulating through the gills and its entry, under the appropriate pressure, into the swimbladder, it is clear that considerable energy will be required to concentrate the gas. By using the energy of compression equation, Parr (1937) calculated that, to fill its swimbladder to the requisite buoyant volume, a fish living at a depth of 1000 m. would use 300 times as much energy as the amount it would need at 10 m. While appreciating this, Bruun (1943) pointed out that the *absolute* amount of energy needed is quite small. He expressed it thus: 'If we take an adult *Spirula* of a weight of 10 g. and with a shell containing about 0·5 ml. gas, it would cost about 13 g. calories to fill it at 2000-m. depth, corresponding to only a few mgs of food.' Looking at the problem from much the same aspect, Scholander (1954) has calculated that for each part of oxygen secreted into the swimbladder a minimum of 3 per cent must be diverted to the work of compression. Like the compressibility factor, it would thus seem that the energy problem is not so serious as it might first appear.

GAS REQUIREMENTS OF THE SWIMBLADDER

While the proportion of oxygen needed for the energy of compression seems not to be excessive, gas must be available in sufficient quantity, if the swimbladder is to be kept inflated at the volume for weightlessness in water. The greater the depth the more the gas needed for a given unit of buoyancy (see pp. 89–90). But it should be remembered that most species of bathypelagic fishes have swimbladders with a capacity of 0·5 ml. or less. On the other hand, many of these fishes move up and down in the sea each day. As these migrations take place within the upper 1000 m. of the ocean, the effects of pressure on gas-density need not be considered. (At 500 m. the density of oxygen is about 0·07.) But as it swims downwards to regain its daytime station, the main physical stress facing a fish is the provision of enough oxygen to fill the swimbladder. From this general introduction we may turn to the physical and biological aspects of vertical migration.

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[1] The swimbladder also contains nitrogen (from about 2 to 15 per cent), argon and carbon-dioxide. If the partial pressure of CO_2 ever reached 50 atmospheres, which from the papers cited, seems unlikely, it would exist as a liquid at temperatures of 13° C. and below.

THE PHYSICS AND BIOLOGY OF VERTICAL MIGRATIONS

After reviewing the evidence for the daily changes in the vertical disposition of bathypelagic fishes, some appreciation of their physical and biological environments will be given. In moving up and down, these fishes are following inner urges, and in so doing are exposing themselves to changing physical and biological conditions. Discussion of these aspects forms the third part of this section and leads to the final one, which centres around the vertical distribution of pelagic and benthic deep-sea fishes with a swimbladder.

THE EVIDENCE FOR VERTICAL MIGRATIONS

Study of the deep-sea fishes taken by the 'Challenger' (1872–6) led Günther (1887) to regard species with well-developed luminous organs and eyes as nocturnal surface-swimmers, which during the daytime, withdraw to the darkness of the deeper waters. The 'Valdivia' (1898–9) and 'Gauss' (1901–3) took numerous luminous fishes in surface-nets at night, and both Brauer (1906) and Pappenheim (1914) concluded that many deep-sea fishes regularly seek the surface-waters during the hours of darkness. The fishes they listed include several species of myctophids, *Astronesthes niger*, *Idiacanthus fasciola*, *Stomias affinis* and certain melanostomiatids.

Murray and Hjort (1912) also found that *Astronesthes niger* and *Idiacanthus* could be taken at the surface during the night. Moreover, the hauls of the 'Michael Sars' enabled Hjort to be more precise concerning the vertical migrations of *Gonostoma elongatum* and *Photostomias guerni*. During the day both species were only to be found in nets fished at 500 m. and below, but at night were taken between 150 and 500 m. Jespersen (1915) was also able to analyse the diurnal changes in distribution of *Argyropelecus hemigymnus* in the Mediterranean. Daytime hauls revealed that the populations were centred below 500 m., whereas at night the main concentrations were between about 150 and 500 m.

The Dana Expeditions fished many nocturnal nets, and scrutiny of the papers concerning the fishes (Regan and Trewavas, 1929, 1930; Ege, 1934, 1948) shows that numerous stomiatoids were taken in the upper 50 m. during the night. However, many species were not caught in these near surface-nets. Considering only the former and the commoner records, the following are evidently nocturnal surface fishes: Astronesthidae; *Astronesthes niger*, *A. indicus*, *A. filifer*, Melanostomiatidae: *Eustomias obscurus*, *E. brevibarbatus*, *E. macrurus*, *Bathophilus metallicus*, *B. pawneei* and *Melanostomias spilorhynchus*; Stomiatidae, all species, except *Stomias nebulosus* and *S. colubrinus*; Idiacanthidae, *Idiacanthus fasciola*; Chauliodontidae, *Chauliodus danae*, Malacosteidae, *Photostomias guerni* and *Aristostomias polydactylus*.

However, by far the commonest fishes in the surface-waters at night are the Myctophidae. Many, but seemingly not all, species can be netted at the surface after sunset. In the eastern tropical Pacific, Beebe and Vander Pyl (1944) studied the migration of various species, particularly *Gonichthys coccoi*. By day, the schools were centred about 400 m., but just after dark the fishes appeared at the surface, where they swarmed between 7.0 and 10.0 p.m. Thereafter, they appeared to disperse or withdraw from the surface, but were still caught there until 6.30 a.m., when they withdrew to their daytime levels.

The other species that massed near the surface after dark included *Lampanyctus macropterus*, *L. omostigma*, *Myctophum affine*, *M. aureolaternatum*, *M. evermanni*, *M. laternatum*, *M. reinhardti*, *Notolychnus valdiviae*. But the catches of certain species, notably *Lampanyctus mexicanus*, came from deeper-lying waters at all times of day. Other evidence for diurnal movements in Myctophidae may be found in the papers by Tåning (1918), Tucker, 1951, Grey (1956) and Barham (1957).

Besides the evidence to be got from nets, studies of fishes in relation to deep-scattering layers (Marshall, 1951; Tucker, 1951; Hersey and Backus, 1954; Kanwisher and Ebeling (1957); Backus and Barnes (1957); Johnson, Backus, Hersey and Owen (1956) and Barham (1957)) indicate that bathypelagic species, particularly those with swimbladders, are a conspicuous constituent of these layers. Furthermore, it seems likely that the most prominent of the fish sound-scatterers will prove to be myctophids. Clearly, when surer identification becomes possible, echo-sounders will provide the biologist with a valuable record of these changing events.

In conclusion, a beginning has been made on observing vertical migrations from bathyscaphes. After dives off Villefranche, Trégouboff (1958) wrote as follows: 'La plongée de nuit a permis également d'observer la migration nocturne vers la surface de divers autres animaux, tels que les Crevettes Euphausiacés, lesquelles, ayant quitté leur zone habituelle de 500 m. de profondeur environ, ont apparu en nombre à partir de 100 m. de profondeur. À leur côté chassaient activement, également à ce niveau, des petits *Argyropelecus*, qui se sont maintenus aussi nombreux jusqu'à 250 m., tandis qu'au jour on ne les capture au filet fermant qu'à partir d'au moins de 500 m. Enfin, des petits Myctophidae et quelques *Cyclothone* ont effectué également un déplacement notable vers la surface et se sont montrés, surtout les premiers, en grande quantité déjà entre 200 et 300 m. de profondeur.'

The evidence to be got from nets, sound exploration and bathyscaphes also suggests that the vertical migrations of deep-water fishes differ in extent. However, these findings will best be left until the third part of this section, when the physical problems facing fishes as they move up and down will be considered.

THE PHYSICAL AND BIOLOGICAL ENVIRONMENT

The headquarters of bathypelagic fishes are in the tropical and temperate parts of the ocean. They live below the mixed surface zone, which contains all or the greater part of the actively assimilating phytoplankton, and has an average depth of about 75 m. The lower limit of this zone is marked by a distinct thermocline, which tends to be permanent in subtropical and tropical regions, but is seasonal in temperate waters. Temperatures range from about 10° to 30° C. and salinities from about 32‰ to 41‰.

Below this thermocline comes a transition zone separating the surface mixed layer from the cold, deep water. Iselin (1936) calls this the thermocline layer, for in the warmer parts of the ocean, the temperature drops quite rapidly from about 20° C., its value just below the near-surface thermocline, to about 5° C. at about 1000 m. Taking the level of the lower thermocline to be the depth at which the rate of change of temperature is greatest, in the North Atlantic it is in this lower transition zone that the values of dissolved oxygen begin to fall towards the minimum value. But over much of the eastern tropical Pacific north of the equator, the fall in quantity of dissolved oxygen begins below the upper thermocline, and a thick oxygen minimum layer (containing less than 0·25 ml. l.) is found between depths of 100 and 1000 m. (Wooster and Cromwell, 1958). Conditions appear to be similar over the central area of the equatorial Indian Ocean, where there is an equally thick oxygen minimum layer (with values 1·0 ml. l. or less) between much the same depth-intervals (Sverdrup, Johnson and Fleming, 1942). In the Atlantic, the lowest values (1·5 ml. l. or less) are centred at a depth of about 400 m., below the North and South Equatorial currents (Riley, 1951).

Turning to submarine light, the thermocline layer contains the twilight zone of the ocean. Using a sensitive photomultiplier tube, Clarke and Wertheim (1956) were able to measure the penetration of sunlight down to depths of about 600 m. in clear water off the Western North Atlantic coast. However, the threshold of light for the eyes of many bathypelagic fishes is likely to be well below this level (Denton and Warren, 1957).

While sunlight cannot penetrate far (if at all) below this depth, there is still light from the luminous organs of deep-sea animals (Clarke, 1958). At depths between 1000 and 4000 m., temperatures range from about 6° to 1° C. in temperate and tropical regions, while the quantities of dissolved oxygen are generally above 2 ml./l.

Considering now the biological structure of temperate and tropical oceanic waters, the well illuminated surface waters (down to about 100 m.) form the living-space of the primary producers, the phytoplankton. And, except in the tropical eastern Pacific, these upper layers (from the surface down to about 200 m.) contain far greater quantities of zooplankton than the waters below (Jespersen, 1935; Vinogradov, 1955; Foxton, 1956; Zenkevitch and Birstein, 1956; Bogorov, 1958). Riley (1951) has estimated that the total oxygen consumption and phosphate regeneration below the density surface sigma—t 26·5 (average depth 200 m.) is equivalent to a utilization of about one-tenth of the surface production of organic matter by the plants. Thus, about nine-tenths of this organic production will be consumed in the upper 200 m., and, compared to the average depth of the ocean, this layer is little more than a 'surface film'.[1]

While the waters below 200 m. support sparse populations of zooplankton, there is good evidence of a secondary maximum in the intermediate thermocline layer. In the western North Atlantic Leavitt (1938) found a mid-depth maximum centred at a depth of 800 m. (there was also a lower lying, but lesser concentration at 1600 m.). Jespersen (1935) also found a mid-water maximum of zooplankton (at about 1000 m.) in the tropical Pacific Ocean, whereas in the north-western part it is centred higher in the water at about 500 m. (Bogorov and Vinogradov, 1955). It would seem that the rapid increase of density and viscosity in the thermocline layer slows down the fall of detrital material, so that it tends to accumulate at mid-depths. Such concentrations of suspended material will support detritus-feeding animals and their predators. As Miyake and Saruhashi (1956) have pointed out, oxygen-minimum layers in the Atlantic and Pacific Oceans occur most frequently along the same sigma-t surface (27·2–27·3) and are most marked in the more productive regions. However, in the equatorial Pacific (Albatross stations III–123, between 0° and 15° N.), Jerlov (1953) found a mid-depth maximum of suspended particles between 700 and 800 m., a level 150 m. below the centre of the oxygen-minimum layer.

Below these rather slight mid-water concentrations, the biomass of zooplankton is small until the bottom waters are reached. The concentration of plankton near the bottom has been repeatedly observed from bathyscaphes (Bernard, 1955; Pérès, Picard and Ruivo, 1957; Pérès, 1958 and Trégou-boff, 1958). Apart from 'microplankton' (some of which is detritus), aggregations of larger forms, such as euphausiids, sergestids and chaetognaths have been seen. (The observations were made in the Atlantic (off Portugal) and in the Mediterranean at depths ranging from 600 to 2200 m. and the layer seems to be about 100 m. in depth.) Such near-bottom concentrations of plankton are likely to be widespread and may at least partly explain Riley's (1951) finding that the rates of oxygen consumption near the deep-sea floor appeared to be larger than those in the main body of Atlantic deep water. At all events, these bathyscaphe observations are a valuable contribution to deep-sea biology.

The time and effort given each day to vertical migrations by countless oceanic animals is one of the most striking features of their biology. But the plants can only actively assimilate carbon in the surface-waters, and the resulting marine pastures support not only the animals that occupy the same living-space, but also those in the underlying waters. Considering the fishes, there can be little doubt that their daily climb towards the surface is a feeding migration. In the western North Atlantic, to

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[1] 'The autotrophic zone has a depth of 200 metres at most and includes less than 5 per cent of the volume of the ocean. Below this zone, life depends on organic matter carried down by organisms sinking from above or by the vertical migrations of animals back and forth between the depths'. Redfield (1958).

take but one instance, it is surely significant that most deep-scattering layers are detected between depths of 300 and 600 m., the levels between which Leavitt (1938) found minimum quantities of zooplankton. It seems most likely that the fishes take what food they can get during the day, but have a proper meal at night. Like the vertically migrating plankton animals, the up-and-down movements of bathypelagic fishes must be governed by the daily rhythm of submarine illumination, a rhythm that can readily be followed by their highly sensitive eyes. As Denton and Warren (1957) have shown, their pure-rod retinae contain visual gold, a pigment with enhanced sensitivity for the deeper pene-trating, blue rays from the sun.

But not every species of bathypelagic fish is able to take direct advantage of the near-surface con-centration of food. Adults of the deeper-living pelagic fishes (Lyomeri, ceratioid angler fishes, *Cyclothone* spp. etc.) are not found near the surface at night. This is also true of many species living in the upper 1000 m. Fishes with tubular eyes (hatchet fishes, *Opisthoproctus*, *Winteria*, *Scopelarchus*, *Evermannella*, *Gigantura*, etc.), are rarely, if ever, taken in nets fished close to the surface. It is thus evident that there are different degrees of vertical migration. These may now be summarized.

A. *Bathypelagic fishes migrating upward to the surface mixed layer.*

These are able to cross the thermocline and have already been mentioned in the first part of this ection (p. 85–86). Certain species of the stomiatoid families, Astronesthidae, Chauliodontidae, Melano-stomiatidae, Stomiatidae, Idiacanthidae and Malacosteidae. Numerous species of Myctophidae.

Of the Astronesthidae, it appears that only species belonging to the genus *Astronesthes* cross the upper thermocline. It is also likely that some of the myctophids (e.g. *Lampadena* spp.) do not reach the surface-layer. The position regarding the smaller gonostomatids (e.g. *Vinciguerria* spp., *Mauro-licus* spp., *Ichthyococcus*) is less certain. While they live for the most part in the upper 500 m. and evidently undertake vertical migrations (Grey, 1955), the larger individuals are not often taken near the surface at night. Perhaps they migrate to levels close below the thermocline.

B. *Partial migrators of the upper* 1000 *m.*

Cyclothone braueri (and probably *C. signata*), Sternoptychidae, various Myctophidae, *Melamphaes* spp. Evidence for the migrations of hatchet fishes has already been given (p. 85), while Grey (1955) has noted that *Cyclothone braueri* and *Melamphaes* spp. are taken at higher levels by night than by day.

C. *Deeper partial migrators*

In the western North Atlantic diurnally migrating deep-scattering layers can be detected down to 1000 m. (Moore, 1958). This may well be near the threshold of light for the highly sensitive eyes of deep-water fishes (see above). In discussing this problem, Clarke (1958) wrote as follows: 'A depth of about 900 to 1000 m. would appear to be the shallowest level in clear water at which day and night changes in illumination would be below the threshold of perception and at which daylight would never be sufficiently strong for the inhabitants to be seen by their predators or by their prey.' Diurnal migrations geared to submarine sunlight would thus seem to be confined to the upper 1000 m. of the subtropical and tropical ocean. In temperate waters the threshold must be nearer the surface.

But certain of the deeper-living fishes seem to undertake vertical migrations. Off Bermuda, Grey (1955) found that the daytime catches of *Cyclothone microdon* came from nets fished between 800 and 2000 m., while at night the upper level rose to 250 m. The populations of *Cyclothone pallida*, *Melam-phaes microps*, *M. opisthopterus* and *M. robustus* also occupied higher levels at night. It may be that

vertical migrations were confined to these individuals that were living by day above the threshold of light. However, there is a distinct possibility that the deeper living fishes may be migrating upwards to the mid-water concentration of plankton, which is centred at levels between 500 and 1000 m. (see p. 87). Considering the plankton maximum at 800 m. in the western North Atlantic, this could mean that the diurnal movements of the fishes living below this level were taking place without the cues provided by submarine sunlight. However, it was in this area and at a depth of 900 m. that Clarke (1958) found a maximum in the frequency of luminescent flashes from deep-sea animals. Furthermore, Kampa and Boden (1957) have found a diurnal rhythm in the mean frequency of flashes from animals in a sound scattering layer in the San Diego trough. The frequency was least at midday, greatest during the twilight migration of the layer and maintained at an intermediate level during the night. If this rhythm proves to be common to all diurnally migrating, deep-scattering layers (and these occur down to at least 800 m.), it might well be the cue for the upward migrations of the deeper living fishes. Zenkevitch and Birstein (1956) visualize a ladder of migration extending to very deep levels down which organic matter produced at the surface is conveyed to the greatest depths. Perhaps luminescent light will prove to be as important as sunlight in maintaining the daily movements up and down the ladder. Recently, Nichol (1958) has estimated the maximal distance at which the light of various marine animals can be seen in seawater by eyes that can just perceive light of $1\cdot6 \times 10^{-10}\mu$ w/cm². In very clear water the distances vary from 6 to 170 m., and luminescent flashes have been detected down to a depth of 3750 m. (Clarke, 1958).

PHYSICAL PROBLEMS

Against this background of their physical and biological environment, we may now turn to the physical stresses that face a fish moving up and down in the water column. Clearly, these will depend on the extent of its vertical displacement. In considering the migrations of fishes with swimbladders, they may be divided as before into thermocline crossers, those that pass through the upper thermocline into the surface mixed layer, and partial migrators, those that remain below the thermocline.

THERMOCLINE-CROSSERS

Gas secretion

While fishes are diving to their daytime levels, the pressure exerted on the swimbladder gases will increase by 1 atmosphere for every 10 m. of the descent. An adult of one of the larger myctophids, e.g. (*Myctophum punctatum*) weighs about 5 g. and the capacity of its swimbladder will be about 0·25 ml. If it moves from 10 to 300 m. and produces no gas during the descent, the volume of the swimbladder will be compressed to 0·017 ml. To inflate the sac to the requisite capacity it must produce about 0·23 ml. gas at a pressure of 30 atmospheres or 6·9 ml. at one atmosphere, the pressure of dissolved gases in seawater. Supposing the fish to have an oxygen consumption of 1 ml. hr., the physical problem of secretion seems insuperable.

Using the energy of compression equation as a basis for their calculations, Kanwisher and Ebling (1957) have considered the physiological effort needed. They take a 10-g. fish with a 0·4 ml. swimbladder and an oxygen consumption of 0·4 ml. hr. Assuming that one-third of the blood circulation is available for the swimbladder and the efficiency of the secretion process is 25 per cent, they compute that 33 hr. secretion would be needed to restore buoyancy after a migration from the surface to a depth of 400 m. But judging from the movements of deep-scattering layers, the time taken for the downward migrations would be not much more than 1 hr. and (presumably) the fish will ascend again in about 12 hr.

Perhaps the figure for the oxygen consumption is too low. Job (1955) found that a 5-g. *Salvelinus fontinalis* will take up 1 ml./hr., and from his graphs the figure for a 10-g. fish would be about 1·2 ml. But the oxygen requirements of an alpine char are not necessarily those of a lantern fish. However, it is clear that lantern fishes are very active. Summing up his bathyscaphe observations, Pérès (1958) wrote the following concerning these fishes: 'Les individus sont presque sans cesse en mouvement, mais dans les directions les plus variées.' Furthermore, they have a relatively large expanse of gill surface. Using Gray's (1954) procedure, I have measured the gill-surface of two *Myctophum punctatum*, both with a weight of about 5 g. The number of gill-lamellae per millimetre of gill-filament is about 50 and the gill area per gram of body weight is 600–700 mm.[2] Comparing this figure with those got by Gray and those listed by Fry (1957), this lantern fish can be put among the active species with a relatively large gill surface.[1]

There is a further aspect. The catches of the 'Michael Sars' led Hjort (1935) to conclude that the twilight depths of the warm Atlantic were inhabited by a Lilliputian fauna of bathypelagic fishes.[2] This is particularly true of the species with a swimbladder. The adults of most gonostomatids, sternoptychids, *Astronesthes* spp., myctophids and melamphaids range between 20 and 150 mm. in standard length and weigh from about 0·5 to 10·0 g.

Now the oxygen consumption of fishes does not follow the surface rule, nor is it proportionate to weight. When the logarithm of the rate of respiration is plotted against the logarithm of weight, the slope of the curve is less than unity (usually from 0·66 to 0·9). The rate of uptake of oxygen falls between surface-area and weight dependence (Fry, 1957).

Thus, the smaller the species, the greater its oxygen consumption per unit of body weight. This may not mean that extra oxygen would be available for gas secretion, but coupled with the considerable expanse of gill surface in such fishes as the myctophids and *Astronesthes* spp., the idea is not to be dismissed. At all events it is striking that the only predatory fishes with swimbladders which cross the upper thermocline are the species of *Astronesthes*,[3] and there is a marked tendency for the adults of this genus to be smaller than those of other predatory stomiatoids (Chauliodontidae, Stomiatidae, Melanostomiatidae, Idiacanthidae and Malacosteidae), which as we have seen, have no swimbladder.

Lastly, hydrostatic pressure has an effect on the rate of metabolism. Fontaine (1930) experimented on *Pleuronectes platessa*, *Ammodytes lanceolatus*, *Gobius minutus*, and *Anguilla anguilla*, finding that an increase in pressure from the atmospheric level to 100 kg./cm.[2] (1 kg./cm.[2] = 0·968 atm.) enhanced the rate of oxygen consumption by 35–88 per cent. The smaller the fish, the greater was this percentage increase. Using the first species, Fontaine showed that the rate of oxygen consumption steadily rose as the pressure was increased to 125 kg./cm.[2], but thereafter fell rapidly, the fish being killed at a pressure of 150 kg./cm.[2].

A myctophid or astronesthid diving to its daytime level might pass from a pressure of a few atmospheres to one of about forty or fifty. There is thus a possibility that their rate of oxygen uptake would tend to increase with depth. However, it is not certain that deep-water fishes would be influenced in the same way as shallow-water species, although *Anguilla anguilla* spends part of its life as a deep-sea fish. The question can only be decided by comparable experiments on deep-water species.

But even supposing that the oxygen consumption of a 10-g. deep-sea fish (say, a large myctophid)

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[1] *Astronesthes niger*, which is also a thermocline-crosser also has about 50 gill-lamellae per millimetre of gill-filament. *Argyropelecus aculeatus*, presumably a partial migrator, has about 40.

[2] While nets give a limited impression of the size range of a species, bathyscaphe observations do not controvert Hjort's view.

[3] *Astronesthes* spp. seem to have a decided liking for myctophids (Murray and Hjort, 1912; Beebe and Vander Pyl, 1944).

is three times the value taken by Kanwisher and Ebling (1957), the gas secretion time for a downward migration of 100 m. would still be 11 hr. At this rate the fish could just restore its buoyancy to the neutral level between the daily descent and ascent.[1] Moreover, it seems unlikely that the gland could produce oxygen fast enough to keep pace with the increasing pressure during the descent. A striking proof of this may well have been given by Hersey and Backus (1954). While following a descending deep-scattering layer they found that the resonant frequency of the reflected sound increased, as though elements in the nature of gas-bubbles were being compressed. As they remark, the bubbles were probably the swimbladders of fishes.

But if the cells of the gas-gland are able to store oxygen in a combined form, the task of restoring buoyancy would be quickened. As we have seen (pp. 73–75), the gland is highly developed in comparison with the volume of the swimbladder. If, by this means, buoyancy can be regained a few hours after the descent, the remaining hours before the ascent could be given to storing oxygen in the gland. If the cells have not reached saturation level by the time the fish is ready to ascend, it may be that some oxygen could be transported to them during the early part of the climb. Deep-scattering layers are known to rise quite slowly for several hours before sunset (see Clarke and Backus, 1956). During this time the (relative) reduction in pressure could be tolerated without the resorptive part of the swimbladder being brought into play (see pp. 96–97). Thus, while the gland would not be secreting it could be storing oxygen. These considerations are at least in keeping with present conceptions of gas-production. Scholander (1954) is inclined to think that oxygen in compound form may be stored in the gland-cells for intermittent use.

The oxygen secreted into the swimbladder comes from the water passing over the gills. How does a fish obtain enough oxygen if it lives in an oxygen minimum layer during the daytime? To take an extreme instance, and one already cited (p. 86), the oxygen level is below 0·25 ml. l. between depths of 100 and 1000 m. in the eastern tropical Pacific, north of the Equator. It is here that Beebe and Vander Pyl (1944) investigated the diurnal migrations of myctophids.

Thus, apart from the upper 100 m., the waters in this part of the ocean would seem to contain insufficient oxygen for active metabolism. (At 20° C. the oxygen consumption of the goldfish, a tolerant species, starts to fall below an oxygen content of 2·5 mg./l. (= 1·75 ml./l.) (Fry and Hart, 1948).) Apart from the other bodily processes, the maintenance of an oxygen pressure of 40 atmospheres in the swimbladder would be against a diffusion gradient of about 10,000 to 1 (Kanwisher and Ebeling, 1957). This seems a gigantic task.

Active life for fishes in this oxygen minimum layer would seem to pose a physiological dilemma. They would have to work very hard to get enough oxygen and the more active they were, the more oxygen would be required. To consume 0·5 ml. O_2 per hour, a lantern fish or *Astronesthes* would have to pass at least 3 l. of seawater over its gills (assuming that two-thirds of the dissolved oxygen would be taken up by the blood). A fish with a volume of, say 5 ml. would not be capable of pumping 1 ml. of seawater over its gills in a second, or even half this volume. In trout (volume about 900 ml.) Van Dam (1938) found the maximum ventilation-volume to be about 5 ml./sec.

Perhaps the activity of these fishes is largely suspended during the day. It was in the Eastern Tropical Pacific that a single haul of a mid-water trawl yielded over 5000 fishes, most of which were the small lantern fish, *Diogenichthys scofieldi* (Marshall, 1954). This is a phenomenal catch and one is led to wonder whether it might be due to reduced activity. Lantern fishes are not known to concentrate in great numbers in dense schools nor are they easy to catch. Daytime observations from a bathyscaphe might well be revealing.

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[1] There is, of course, no certain evidence that the vertical migrations of any particular individual are carried out day after day. In an adult fish the extent of these displacements may also vary in time and space.

If the activities of these fishes are largely confined to night time, when they are swimming in the well-oxygenated surface waters, it is difficult to see how enough oxygen can be obtained to fill their swimbladders. Use of the gas-gland as an oxygen store would seem to be essential for such fishes. The problem (a most intriguing one), remains.

Gas resorption

During its daily climb towards the surface, a deep-sea fish must lose gas from its swimbladder as the hydrostatic pressure is reduced. While the physical problem is simply the converse of that faced during descent, it is a more critical one. Being overweight is presumably no handicap to a diving fish, but during the rise the swimbladder must be kept from exceeding the volume necessary for neutral buoyancy. If this is not done, the fish will lose control and start to 'balloon' upwards to the surface at an ever-increasing rate. Even predatory fishes without a swimbladder are not entirely free from this problem. Günther (1887) relates how Johnson found a gulper-eel (*Saccopharynx ampullaceus*) floating at the surface. The fish had swallowed a nine-inch, deep-sea gadoid (*Halargyreus*) '...the stomach of which was forced up into the mouth by the distended air bladder, showing how rapidly both fishes must have ascended to the surface'.

As we have seen, most of the migrating fishes with swimbladders weigh between 0·5 and 10 g. Considering once more a 5-g. fish with a swimbladder volume of 0·25 ml., a migration from a depth of 400–50 m. will cause the sac to expand to about 2·0 ml. if no gas is lost. So during the ascent, about 1·75 ml. gas, the greater part of which will be oxygen, must disappear into the blood.

Such problems have been considered by Jones (1951, 1952) and are based on experiments with perch (*Perca fluviatilis*), which, like the deep-sea fishes with swimbladders is a physoclist. Jones (1952) has calculated that a migration from 500 to 100 m. by a physoclist should extend over 34 hr. if the swimbladder is to be kept at the volume of neutral buoyancy. He suggests the difficulty could be overcome if the fish had a small swimbladder (the extra space being filled with fat), or thick, pressure-resisting walls bounding the sac, or if the rate of resorption is 20–30 times that supposed in the perch.

Considering these suggestions, the deep-sea fishes have a reduced swimbladder (compared to the perch) in that they live in a denser medium and so need less buoyant support. In freshwater fishes, the volume of the swimbladder is 8 per cent of the body volume (see Jones and Marshall, 1953). Moreover, the walls of their swimbladders are quite thin (see pp. 60–65). The rate of removal of gas from the sac must thus be high.

The quantity of gas diffusing into a capillary bed will directly depend on: (1) the area of the bed; (2) the rate of flow of blood; (3) the concentration gradient (the difference in tension between the swimbladder gases and those in the blood; (4) temperature. The rate of diffusion will also be inversely related to a 'frictional' component, the thickness and nature of the tissue through which the gases move, and on the size of the gas molecules.[1]

The Lilliputian fauna of bathypelagic fishes have decidedly large expanses of capillaries relative to the volumes of their swimbladders (see the descriptive section, pp. 7–50). In Table 6 this is expressed as a ratio of surface of resorbent area : volume of swimbladder. The swimbladder volume is taken to be 5 per cent of the body volume. The surface-area of an 'oval' is readily calculated (but is a minimal value owing to some collapse of the swimbladder) since it is circular. In the stomiatoid fishes the area of the capillary bed was got by dividing it into convenient sub-areas. This will also be a minimal value.

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[1] Fick's law for diffusion processes is expressed thus: $\dfrac{dn}{dt} = -\dfrac{RT}{Nf} a \dfrac{dc}{dx}$, where dn is the amount of substance diffusing across an area a, in time dt, dc/dx is the concentration gradient, R is the gas constant, T the absolute temperature, f the 'frictional resistance' and N the Avogadro number.

Table 6. *Resorbent surface-area : swimbladder volume ratios in various bathypelagic fishes*

Species (standard length mm.)	Area of resorbent surface (mm.²)	Volume of swimbladder (ml.)	Resorbent area:volume ratio of swimbladder
Stomiatoidea			
Vinciguerria attenuata (43·5)	20	*ca.* 0·08	250
Maurolicus muelleri (22·0)	1·2	0·01	120
Argyropelecus aculeatus (48·0)	9·0	0·06	150
Astronesthes niger (41·0)	15·0	0·05	300
Myctophidae	An oval		
Diaphus rafinesquei (70·0)	30	0·30	100
Myctophum punctatum (71·0)	25	0·25	100
Melamphaidae	An oval		
Melamphaes mizolepis (56·0)	8	0·07	115

These ratios are higher than that found in the perch (using Saupe's (1939) figure for the area of the oval). The two myctophids, the melamphaid and *Maurolicus* have ratios that are at least twice as large as that of the perch. In *Vinciguerria* and *Astronesthes* this factor is 4 and 5 respectively.

Clearly, the concentration gradient in these fishes will be much higher than that ever existing in the perch. At a depth of 500 m. the partial pressure of oxygen in the swimbladder will be some 40 atmospheres, a tension several hundred times greater than that in the blood flowing through the capillary bed. This would indicate that the rate of oxygen removal would be limited by the rate at which blood could flow through the resorbent area.

Now, in myctophids the vein or veins leading from the oval to the cardinal vein are extremely large. Furthermore, the by-pass vessel (or vessels) from the retial artery to the oval can take all the blood that would flow through the retia during gas-secretion. Text-fig. 39 shows two large veins from the oval of *Myctophum punctatum*, and they unite to form a single vessel running to the cardinal vein. In the stomiatoids the resorbent surface is also fed with blood through a by-pass of the retial artery while the venous return is through the venous capillaries of the rete (see pp. 78–79). However, the retial flow will not be a limiting factor, which may be seen by using Poiseuilles' law. For a series of n parallel tubes the resistance to the flow of blood will be proportional to:

$$\frac{(\text{Length of a tube})}{(\text{Number of tubes}) \cdot (\text{Diameter of tube})^4.}$$

Using the figures for the diameter and length of the venous capillaries, and for the by-pass artery and other vessels involved in the capillary bed, it can be shown that the retial capillaries have less resistance than that developed in the larger vessels. It would thus seem that the resorbent vascular system in both stomiatoids and myctophids will carry relatively large amounts of blood over a given time.

Temperature will also play a part, though a small one, in accelerating the diffusion of gas into the capillary bed. In the subtropical and tropical ocean, a fish migrating from a depth of 500 m. to the surface will pass from temperatures of about 8–18° C. to those ranging from 20 to 30° C. Thus over wide areas of the warm ocean the rise in temperature is 10° C. or more. However, in terms of absolute temperature the percentage increase in diffusion rate in passing from 10° to 25° C. is less than 10 per cent.[1]

[1] Taking the rate at 20° C. as unity, the value of the diffusion constant rises 1 per cent per degree (Prosser *et al.* 1950).

Finally the 'frictional resistance' must be very small in the resorbent areas of these fishes. The capillary bed is very close to the gases of the swimbladder (Text-fig. 40), the intervening connective tissue being no more than 1μ in thickness (judging from transverse sections).

Considering only the fishes that are known to cross the near-surface thermocline, the preceding discussion could well indicate that their rate of gas resorption is 20–30 times that of the perch. They have a factor of 2–5 in their favour in resorbent surface volume of swimbladder ratio, and a factor many times this related to the concentration gradient of gas. The unknown factor is the amount of blood the resorbent surface can handle in a given time. However, judging by the ascent of deep-scattering layers (Clarke and Backus, 1956), the time taken to reach the surface (including the slow rise before sunset) is at least 2 hr.
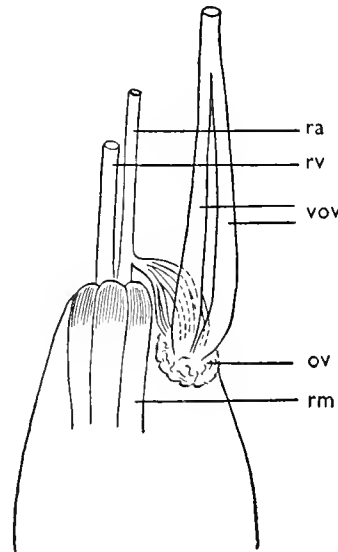
Text-fig. 39. Venous part of the circulation to the oval in *Myctophum punctatum* (× 15). Note the size of the oval veins relative to the retial vein. *ov*, oval; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *vov*, veins to oval.

lumen of swimbladder
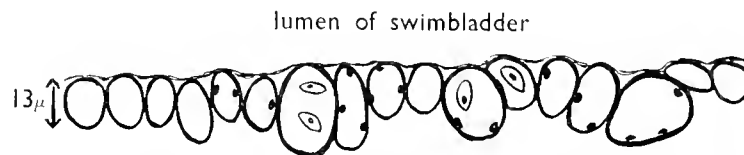
Text-fig. 40. Part of the resorbent capillary network of the swimbladder of *Argyropelecus aculeatus*. Note the very thin layer of tissue separating the capillaries from the lumen of the swimbladder.

PARTIAL MIGRATORS

Gas secretion

During their vertical migrations, fishes that do not penetrate beyond the upper thermocline will be subjected to lesser physical stress than those that go on to the surface mixed layer. A hatchet fish migrating from a depth of 150 to 400 m. is not faced with providing as much oxygen for the swimbladder as a lantern fish moving from 20 to 400 m. However, as we have seen (pp. 74–75) the rete and gas-gland of a hatchet fish swimbladder are highly developed, seemingly as well as those of a lantern fish. In view of the earlier discussion concerning gas-production in thermocline-crossers, this aspect need not be pursued at greater length.

Gas resorption

During its upward migration, the pressure on the same hatchet fish will be reduced by about 60 per cent; the figure for the lantern fish is about 90 per cent. It seems odd that the resorbent surface:swimbladder volume ratio of the hatchet fish *Argyropelecus aculeatus* is greater than the values for the two lantern fishes (see Table 6). But as already suggested, the figures for the two lantern fish in Table 6 are likely to be low. If the radius of their 'ovals' was actually 4 mm. instead of 3 mm., which may well be under natural conditions, the ratios would be about 170 instead of 100. For it is a striking fact that lantern fishes brought up in nets hardly ever have the viscera pushed into the mouth by extra expansion of the swimbladder, whereas this is not uncommon in hatchet fishes. It is also interesting that *Astronesthes niger*, which appears near the surface by night, has a much higher ratio than *Argyropelecus aculeatus*, a partial migrator.

PELAGIC AND BENTHIC FISHES, THE SWIMBLADDER, AND ASPECTS OF THE ECONOMY OF DEEP-SEA LIFE

There is a far-reaching correlation between the focal depths of the living-space and the presence or absence of a swimbladder in fishes from the mid-waters of the ocean (pp. 82–83). While a highly developed, gas-filled swimbladder is found in about half the species that swim in the upper reaches (200–1000 m.) of this environment, this organ is absent or regressed in all fishes with populations centred below the 1000-m. level. Is such a relationship with depth also found in fishes living on or near the deep-sea floor? The surprising fact, as already indicated, is that much of the answer is in the negative.

The main families to be considered are the Alepocephalidae, Bathypteroidae, Harpadontidae, Ipnopidae, Synaphobranchidae*, Halosauridae,* Notacanthidae*, Moridae*, Macrouridae*, Zoarcidae, Brotulidae*, and Liparidae. In the families marked with an asterisk, a swimbladder is commonly present, but is absent in the others. Using Grey's (1956) list of species that are found below a depth of 2000 m., at least half of a total of some 240 species should have swimbladders.

Before giving special consideration to those species that range into the deeper, abyssal parts of the ocean, appreciation is due to observers in bathyscaphes and to underwater photography. Until these records were available, there was always the possibility that some of the supposedly benthic fishes might not live near the bottom. Hjort (Murray and Hjort, 1912), believed that the Bathypteroidae were mid-water fishes, but they have now been seen actually resting on the bottom, supported by the two long pectoral rays and the single, elongated caudal ray (Houot and Willm, 1955). Representatives of the Halosauridae, Moridae, Macrouridae and Brotulidae have also been observed near the bottom (Fages *et al.* 1958; Pérès, Picard and Ruivo, 1957). I have seen halosaurid, notacanthid and morid fishes in photographs of the deep-sea floor taken by Dr A. S. Laughton of the National Institute of Oceanography.

Nybelin (1957) has listed the species that have been fished below a depth of 3000 m. There are sixty-eight. (Alepocephalidae (7), Harpadontidae (2), Bathypteroidae (3), Ipnopidae (3), Synaphobranchidae (3), Halosauridae (2), Notacanthidae (1), Macrouridae (16), Zoarcidae (1), Lycodidae (2), Brotulidae (25), Liparidae (3).) Thus forty-seven species may at least be suspected of having swimbladders.

However, there is the possibility that the deeper living species might have lost this organ. Yet Günther (1887) found a swimbladder in *Typhlonus nasus*, taken by the 'Challenger' at depths of 3934 and 4465 m., and in *Acanthonus spinifer*, trawled at 3242 m. Besides these two brotulids, a

swimbladder is found in the deep-sea eel *Synaphobranchus kaupi* (= *S. pinnatus*) (Scholander and Van Dam, 1954) (depth range: 200–3599 m.) and in the macrourid, *Nematonurus armatus* (Hagman, 1921) (281 to 4600 m.). 'At least forty-six of the more than seventy-six specimens recorded were caught between about 2600 and 3660 m.' (Grey, 1956).

In view of these findings I have examined the following species, the depth range[1] of which appears after the scientific name: Moridae, *Antimora rostrata* (403–2904 m.); Macrouridae, *Lionurus filicauda* (2515–4846 m.); Brotulidae, *Aphyonus gelatinosus* (2550–4360 m.); *Typhlonus nasus* (3932–5090 m.); *Mixonus laticeps* (3200–4575 m.); *Bassozetus taenia* (4575–5610 m.) and *Bassozetus compressus* (1920–2744 m.). Except in *Aphyonus gelatinosus* and *Typhlonus nasus*, each of these species has a capacious swimbladder extending down the greater part of the body cavity. Drawings of some of them appear in Text-fig. 41.

Thus a well-developed swimbladder is present in fishes that may range down to depths of about 5000 m. This is remarkable in view of the previous discussion concerning the compressibility of gases (p. 84). At a depth of 5000 m. the density of oxygen is about seven-tenths that of seawater.

A fish with a fully developed swimbladder containing oxygen would require tissues with a density of about 1·04 to be neutrally buoyant at this depth. But this requirement may well be met. These deeper-living fishes have rather lightly ossified skeletons and the muscles sheathing their flanks are fairly thin. In Pl. 3 a radiograph of *Lionurus filicauda* is shown against one of the poor cod, *Trisopterus minutus*, a shallow-water fish. It will be seen that the skeleton of the cod is more sharply revealed than that of the macrourid:[2] there is also a striking difference in the size of the otoliths. Denton and Marshall (1958) have shown that the density of fish muscle is relatively high, which is not surprising in view of the heavy protein molecules that are required for contraction. In bathypelagic fishes without a gas-filled swimbladder, reduction of muscle and bone can bring the animals close to neutral buoyancy.

The swimbladders of these fishes are also remarkable in having extremely long retia mirabilia (see Text-fig. 41). In *Lionurus filicauda* there are six retia, each having a length of at least 20 mm. The two retia of *Bassozetus taenia* are about 25 mm. long, while the single one of *B. compressus* has a length of 17·5 mm. In the deep-sea eel, *Synaphobranchus kaupi*, the span of the rete is about 10 mm. (Scholander, 1954).

These findings are surely significant in view of the previous discussion on retial length and the efficiency of gaseous exchange between the arterial and venous capillaries (pp. 70–72). As we saw, the deeper the living-space the longer should be the length of the capillaries. This is strikingly revealed in Table 7. (The data for *Antimora viola*, blue hake; *Sebastes marinus*, rose fish; *Nezumia bairdii*, common rat-fish; and *Synaphobranchus kaupi* are taken from Scholander and van Dam (1954) and Scholander (1954).)

Apart from the general trend, which is quite evident, it is interesting that the deeper living of the two *Bassozetus* species has the longer retia, and two in place of one. Here, then, is indication that the swimbladders of abyssal fishes may well be functional at great depths.

But the gas-glands do not appear to be highly developed, which might suggest that their function is simply to keep the swimbladder 'topped up' with gas. Abyssal fishes are unlikely to move very far from the deep-sea floor, except perhaps during the breeding season, although they could have a relatively wide freedom of movement in the vertical plane. If the upper limit of this zone is marked by a pressure reduction of 20 per cent (Jones, 1952), an abyssal fish with a closed swimbladder and in

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[1] Depth-range data have been taken from Grey (1956), Nybelin (1957) and Bruun *et al.* (1956).

[2] The 'Challenger' fishes were preserved in alcohol so there is no danger of the degree of ossification being reduced.

hydrostatic equilibrium at a depth of 4000 m., could swim upwards for 800 m. without the need to lose gas. When it descended there would be no extra gas to find.

These abyssal fishes have not retained their swimbladders simply to solve problems in the second law of thermodynamics. A fish with a swimbladder is able to remain poised off the bottom without undue effort and it can thus devote a greater part of its energy to seeking its food. If a near-bottom
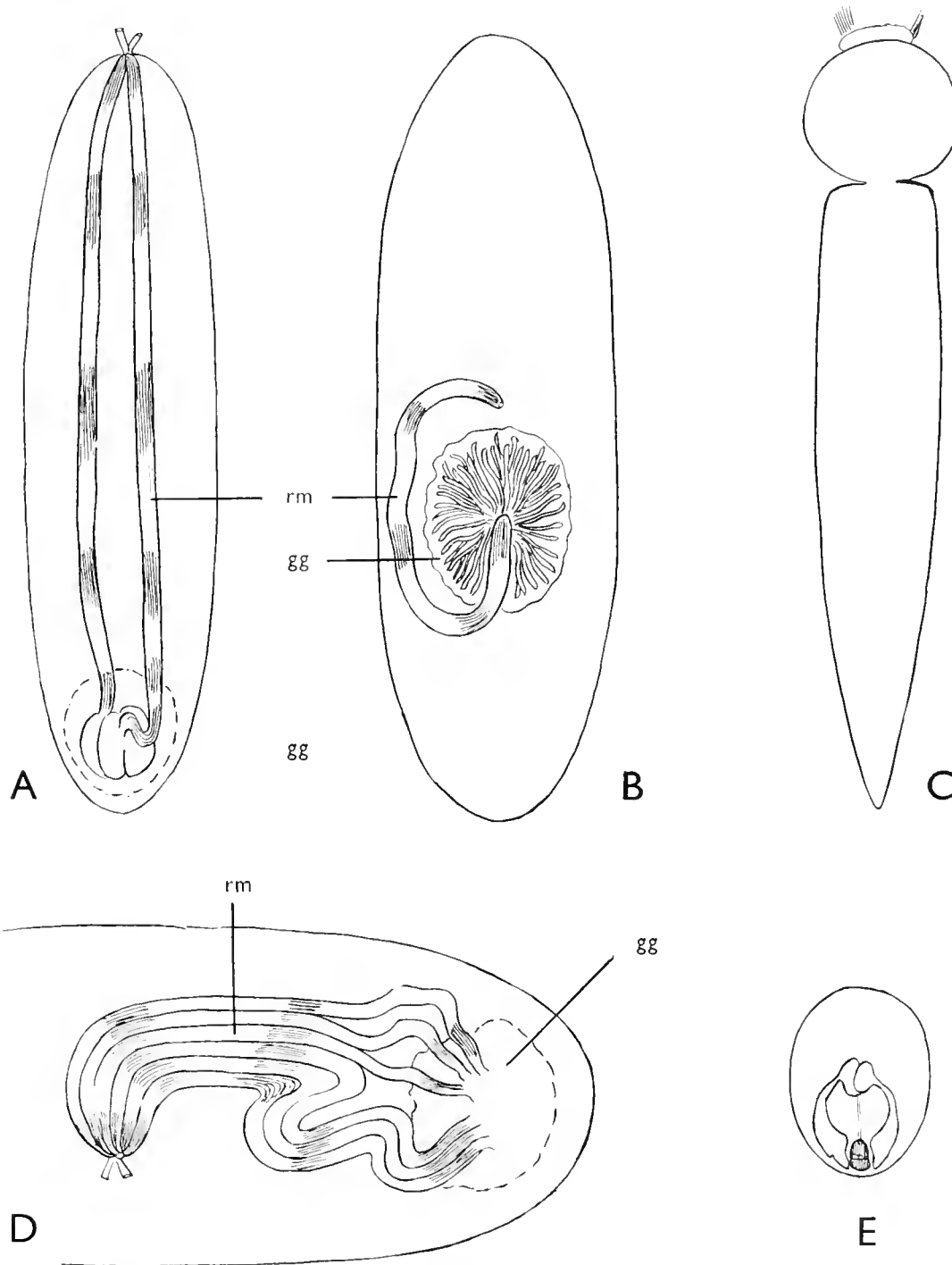
Text-fig. 41. Swimbladders of (A) *Bassozetus taenia*; (B) *B. compressus*; (C) *Antimora rostratus*; (D) *Lionurus filicauda*; (E) *Argyropelecus aculeatus*. In the two species of *Bassozetus* and *Lionurus filicauda*, note the extremely long retia mirabilia, which may be compared with the rete of *Argyropelecus*. Note also the capillary loops in the gas gland of *Bassozetus compressus*. *gg*, gas-gland; *rm*, rete mirabile. (A, × 3·6; B, × 3; C, × 0·7; D, × 3; E, × 3.)

13   D M

Table 7. *Length of retia and the depth range of some deep-sea fishes*

Fishes	Depth range (m.)	Length of retia (mm.)	Number of retia
Bathypelagic species			
Stomiatoidea	200–1000	0·75– 4·0	1
Myctophidea	(centres of concentration)	1·5 – 4·0	3
Benthic species			
Sebastes marinus	30–1680	7·0 –10·0	?
Antimora viola	560–1830	7·0 –10·0	?
Stephanoberyx monae	–2295	8·0	2
Nezumia bairdii	140–2300	7·0 –13·0	?
Bassozetus compressus	–2744	17·5	1
Synaphobranchus kaupi	200–3599	10·0	1 ?
Lionurus filicauda	2515–4846	20·0*	6
Bassozetus taenia	4575–5610	25·0	2

concentration of plankton is also found over the abyssal plain, such a fish could take full advantage of this food as well as that on and in the sediments. Macrourids plough up the oozes, no doubt in search of food, and they also take planktonic forms such as euphausiids, sergestids and copepods (Marshall, 1954). Bathypteroid fishes, which have no swimbladder and come to rest on the oozes after swimming, may be more limited in their choice. A radiograph of one of these fishes showed the skeleton to be well ossified and, as the myotomes are compact and well-developed, they are undoubtedly heavier than their environment, which as Jones and Marshall (1953) point out, is no handicap to a fish living on the bottom. But the more striking fact is that about two-thirds of the fishes that range below 3000 m. have swimbladders.

Besides its buoyant effect, the swimbladder can also be used to produce sounds. Certain species of macrourids have special drumming muscles attached to the swimbladder, but sounds can be made without such aid (Marshall, 1954). The gas-filled sac may act as a resonator to enhance the noises produced by neighbouring structures, such as the grinding of the pharyngeal teeth. In the abyssal darkness, sounds might be vitally important for communication between the sexes during the breeding season. After studying certain sounds recorded in deep water, which were like those made by fishes, Griffin (1955) suggested that the 'fish' might use the sounds for echolocation of the bottom. His concluding remarks are interesting: 'Finally it must be pointed out that even though this recording does reveal a fish-call plus its echo from the bottom, we have no direct evidence that the unknown fish could hear such an echo, and still less that it would pay any attention if it did. Yet the "echo-fish" could easily have heard these bottom echoes if it had an auditory sensitivity equal to that of any fish adequately studied to date, and in the unlighted depths of the ocean echolocation could be as advantageous to a fish as it is to a bat flying in darkness through the air.'

By becoming closely associated with the inner ears the swimbladder can also act as a hydrophone. Such association is known in one group of benthic deep-sea fishes, the Moridae, (Svetovidov, 1948) a family containing about seventy species. In other fishes a connection between the ears and swimbladder is correlated with a wide frequency range and low auditory threshold (Jones and Marshall, 1953). At present we can only add that the deep ocean is by no means a silent world.

It must now be evident that there is a striking difference between the development of the swimbladder in the pelagic and benthic fishes of the deep ocean. Taking a vertical section over the deep-sea floor between depths of 2000 and 5000 m., at least half of the pelagic fishes with centres of concentration in the upper reaches (between 200 and 1000 m.) have capacious swimbladders and the same is true of the bottom-dwelling species. But this organ is regressed or absent in the pelagic fishes living in the intervening waters below the 1000-m. level.

The evidence suggests that the swimbladder is perfectly functional in benthic species ranging beyond a depth of 2000 m. Why has this organ been lost in the deeper-dwelling pelagic fishes?

There are many differences between fishes living in the upper and lower reaches of the pelagic environment. Clearly, the most relevant contrasts may be made within genera consisting of species that inhabit both regions. *Gonostoma* is one such genus, and here *G. denudatum* will be contrasted with *G. bathyphilum*.

The populations of the first species are centred above 1000 m., while those of the second are concentrated well below this level. Certain differences between these species have already been considered (Marshall, 1954, 1955; Denton and Marshall, 1958).

Gonostoma denudatum has a capacious, gas-filled swimbladder, but there is no trace of this organ in *bathyphilum* (p. 13). Radiographs of the two fishes show the skeleton of the first species to be more heavily ossified than that of the second. Furthermore, the flanks of *denudatum* are sheathed with well-formed scales, while the skin of *bathyphilum* is naked. Correlated with the firmer skeleton, the myotomes of *denudatum* are more compact and extensive than those of *bathyphilum*. This is particularly evident along the post-anal part of the body, which is slimmer and less robust in *bathyphilum* (see Text-fig. 42).

By comparison with *bathyphilum*, the eyes and light organs of *denudatum* are highly developed. In fishes of the same size, the diameter of the eye in the former is rather less than half that of the latter, and there is a striking difference in the relative development of the dioptric parts (Marshall, 1954). Reference to Text-fig. 42 will show the extraordinary contrast in the size of the photophores.

Having proportionately larger eyes, it is not surprising that *denudatum* has larger optic lobes. But this difference in emphasis extends to all parts of the brain (see Text-fig. 42). Particular attention may be drawn to the corpus cerebellum, the volume of which in *denudatum* is about double that of *bathyphilum* (Text-fig. 42). Now there seems to be a direct correlation between the degree of development of this nervous centre and locomotor activity (see Healey, 1957; Kurepina and Pavolovsky, 1946), which would suggest that *G. denudatum* is the more active species. As we have seen, the myotomes of this species are better developed.

Parallel differences are also found in the gill-system. In *G. denudatum* the four gill-arches bear filaments along their entire length. In the specimen drawn in Text-fig. 42 the average length of the filaments on the second arch is about 2 mm., and there are some six filaments to each millimetre of the arch. The filaments bear about 60 lamellae per millimetre.

Conditions are very different in *G. bathyphilum*. On the first gill-arch the filaments are confined to the forward part of the lower arm, while on the other arches they occur along the entire extent of the lower arms. The filaments are short and feathery (about 1 mm. long and three or four per millimetre along the second arch). The number of lamellae on a 1-mm. filament is about 20–25. While there is the possibility that the skin of *G. bathyphilum*, being scaleless, might assist in respiration, there is striking indication that the tissues are much regressed by comparison with those of *G. denudatum*.

Finally, this economy of living substance in *bathyphilum* is also revealed in the size of the kidneys, which in *Gonostoma* consist of paired anterior parts joined by thin bridges of tissue to an unpaired posterior part. Comparison of a *G. bathyphilum* (standard length 77·5 mm.) with a *G. denudatum* (standard length 81·5 mm.) showed that the kidneys of the latter have a more compact appearance and are much larger than those of the latter. (The anterior parts in both species have much the same length (7·0 mm.) but those of *denudatum* are more voluminous. The posterior parts of the kidneys of *denudatum* are larger by a factor of about three.)

Now in teleosts the simpler products of catabolism (ammonia and urea) tend to be excreted by the gills, while the more complex products (creatine, creatinine and uric acid) are dealt with by the

kidneys. But as both gills and kidneys in *bathyphilum* are greatly reduced, there can be little doubt that *denudatum* is the more highly organized and active species.

The species of *Cyclothone* also live at different levels in the ocean. *C. braueri*, a light-coloured species, occurs mainly between 500 and 1000 m., while the populations of the black species (*livida*,
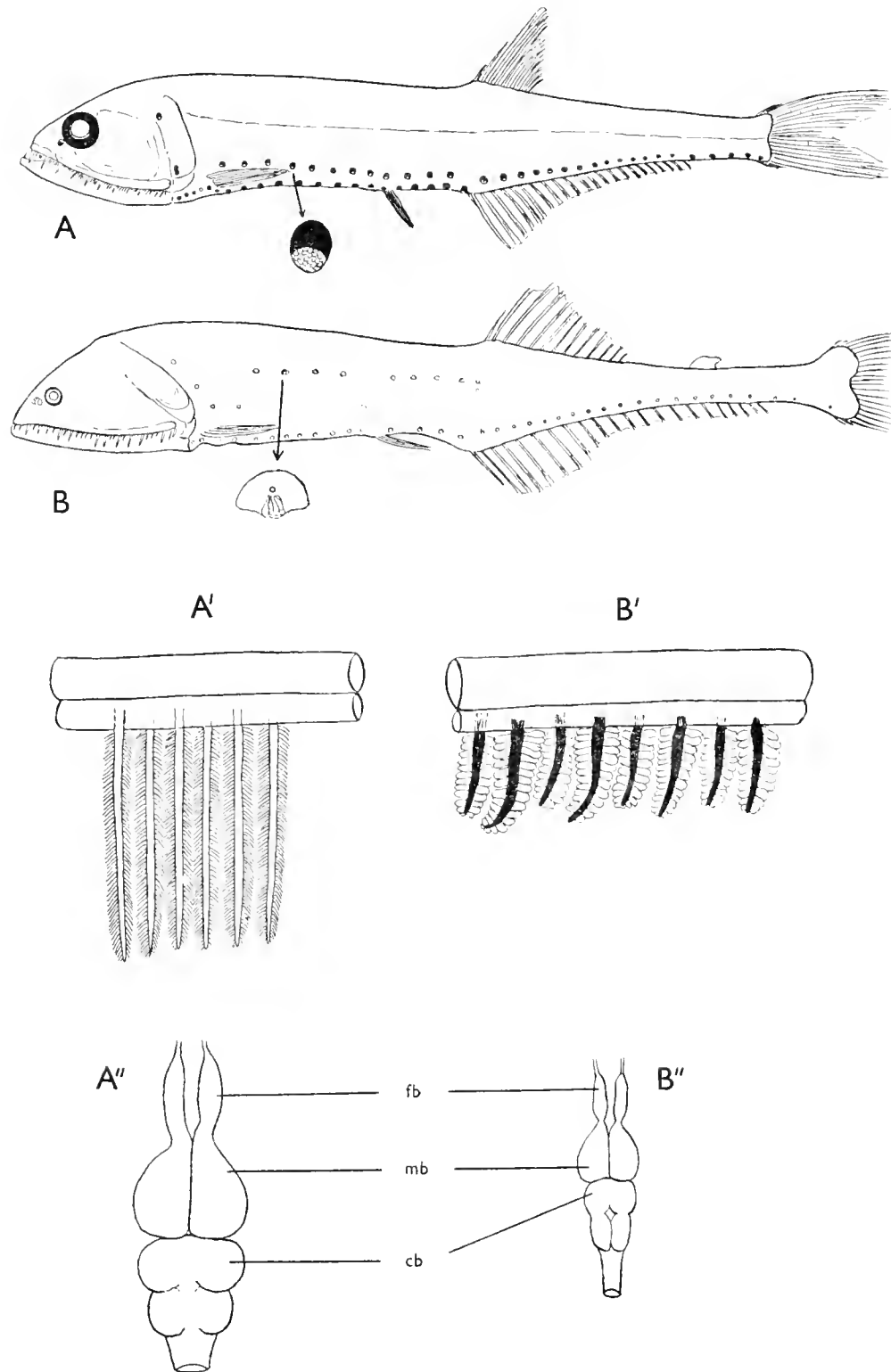
Text-fig. 42. Comparison of the external appearance, gill development and brain of *Gonostoma denudatum atlanticum* (A, A′, A″) and *G. bathyphilum* (B, B′, B‴). The gill filaments shown in (A′) and (B′) are from the second gill arch. *fb*, forebrain; *mb*, midbrain; *cb*, cerebellum. (A and B, ×0·75; A′ and B′, ×12·5; A″ and B″, ×5.)

microdon, acclinidens and *obscura*) are centred at levels of 1000 m. and below. Of the forty-four recorded specimens of *obscura*, only three came from nets fished above a depth of 2000 m. (Grey, 1956), while *C. microdon* is common between levels of 1000 and 2000 m. (Murray and Hjort, 1912). We may thus compare the three species *braueri*, *microdon* and *obscura*, as they seem to occur at increasingly deeper levels.

During the larval phase, which is passed in the surface waters, a gas-filled swimbladder is present in the species *braueri* and *microdon*, but the organ regresses and becomes invested with fat after metamorphosis (pp. 65–66). Knowledge of the life-history of *obscura* matches its trivial name.

C. braueri and *C. microdon* grow to about the same size (70 mm.), but there is some evidence that the regression of the swimbladder occurs at a later stage in the former. At a length of from 30 to 35 mm., the swimbladder of *braueri* is beginning to regress but a cavity is still present, while in *C. microdon* of this size regression is almost or quite complete.

Besides this difference, which requires closer study, the degree of development of the eyes and light-organs forms a graded series in the three species. This was first appreciated by Brauer (1908) and also considered by Hjort (Murray and Hjort, 1912).[1] It will be seen that the eyes are largest in *braueri*, as compared with *microdon*, which has medium-sized eyes, while those of *obscura* are extremely small. The same is true of the photophores. It should be added that Brauer regarded the light organs of *C. obscura* to be rudimentary and found some of them to be absent.

Having no specimens of *C. obscura*, I have only been able to compare the brains of *braueri* and *microdon*, which came from individuals of about the same size (25 mm.). Drawings of these appear in Text-fig. 43. Measured from the tip of the forebrain to the end of the cerebellum, both brains have much the same length (2·0 mm.). But the optic lobes and, evidently, the cerebellum of *braueri*, are considerably larger, the width of the former being 1·1 mm. in *braueri* and 0·7 mm. in *microdon*.

Comparison of the gill-system of these two specimens is also revealing. In both species, filaments are borne on the lower arms of the first, second and fourth arches, but on only the forward half of this part of the third arch. In *C. braueri* the filaments are both larger and more numerous, there being 12 per mm. on the first arch, compared to nine in *microdon*. Reference to Text-fig. 43 will show the difference in filament size.

To summarize, in these three species of *Cyclothone*, the deeper the living-space, the less the development of the eyes, photophores, brain and gills. Since the greater part of the populations of *C. braueri* live above the threshold of light, while both *microdon* and *obscura* are most common below this level, the relatively large eyes and photophores of *braueri* might seem to be related to an existence in the twilight zone. But this factor cannot be invoked to account for the marked difference in eye and photophore development of *microdon* and *obscura*. Some factor (or factors) related to the deeper living-space of *obscura* would seem to be involved.

To conclude these studies of related fishes, two species of the family Gonostomatidae will be considered, *Maurolicus muelleri* and *Cyclothone microdon*. *Maurolicus* is most abundant above a level of 500 m. (Koefoed, 1958) while *C. microdon*, as already indicated, is mostly to be found below 1000 m. The first species has a well-developed gas-filled swimbladder, while in *Cyclothone* this organ is obliterated in the adult phase.

Drawings of these two fishes may be found in Text-fig. 44. The much greater development of the eyes and light-organs of *Maurolicus* will be immediately obvious. The myotomes of this fish are also much more compact and extensive. In a well-nourished *Cyclothone microdon*, the myotomes appear at first sight to be more voluminous than they actually are. Much of the space between the skin and

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[1] The species that Brauer took to be *Cyclothone signata* Garman proved to be a separate species, which was called *C. braueri*, by Jespersen and Tåning (1926).
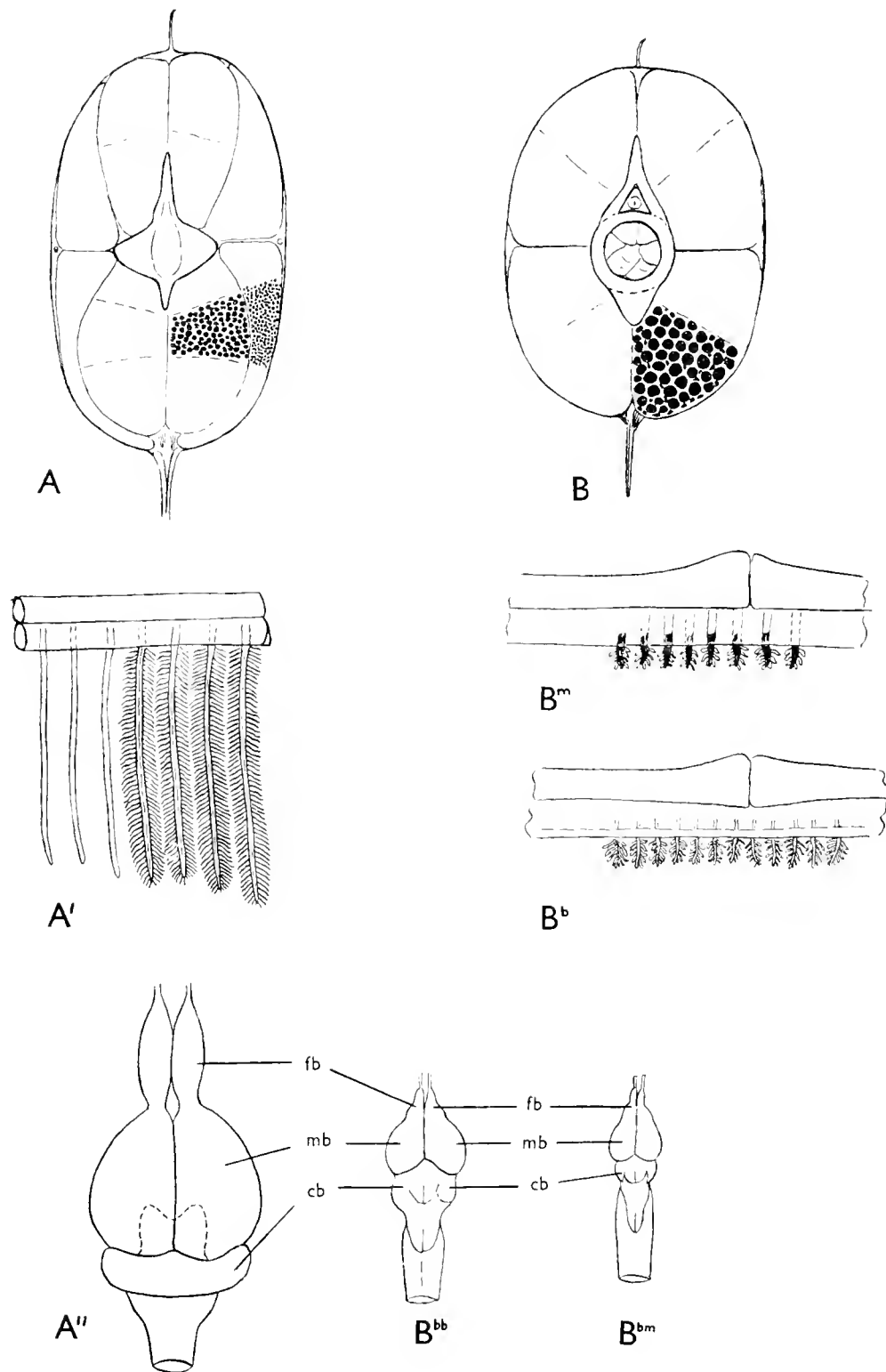
Text-fig. 43. The development of the body muscles, gill filaments and brain of (A, A′, A″) *Maurolicus muelleri*; (Bᵇ, Bᵇᵇ) *Cyclothone braueri*, and (B, Bᵐ, Bᵇᵐ) *C. microdon*. In A and B, which are transverse sections through the body just in front of the caudal peduncle, the muscle fibres are shown in black and are drawn to scale. The drawings of the gill filaments are from the lower part of the first gill arch. *fb*, forebrain; *mb*, midbrain; *cb*, cerebellum. (A, B, ×15; A′, Bᵐ, Bᵇ, ×20; A″, Bᵇᵇ, Bᵇᵐ, ×9.)

myotomes is taken up by extensive fat sinuses, which are especially capacious along the back between the head and the dorsal fin. Subcutaneous fat sinuses also occur between the pelvic and anal fins, between the muscles moving the dorsal and anal rays, and above and below the caudal peduncle. The drawing of the fish in Text-fig. 44 B is actually of the closely related species, *C. pallida*, in which the lack of pigment in the skin makes the sinuses easier to trace.
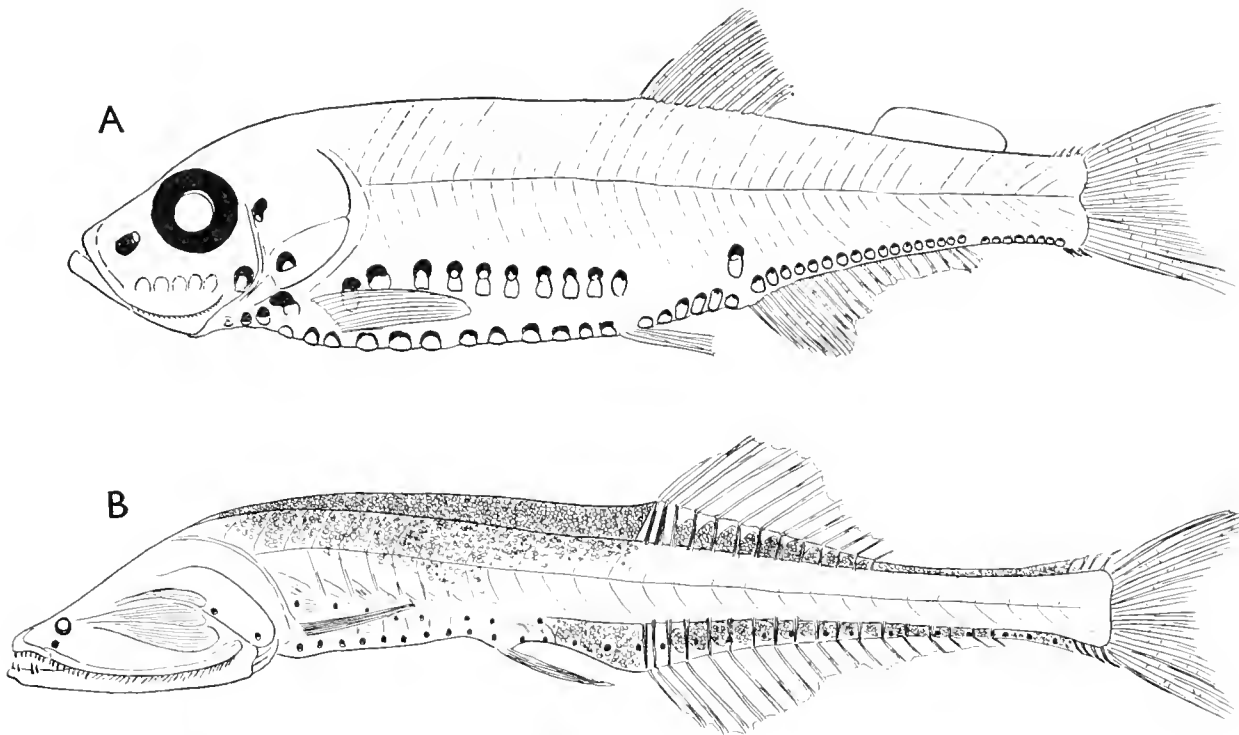
Text-fig. 44. External appearance of (A) *Maurolicus muelleri*; (B) *Cyclothone pallida*. Both, × 3.

Reference to Text-fig. 43 will show that the brain of *Maurolicus* is large compared to that of *Cyclothone microdon*. (The standard lengths of the two fishes measured 35·0 and 36·5 mm. in the order just given.) This is even more true of the gill surface. On the lower part of the first gill arch of *Maurolicus*, the filaments have an average length of 1·5 mm. and there are 5 per mm. The number of lamellae per millimetre of filament is about 50. The first two corresponding figures for *Cyclothone microdon* are 0·2 mm. and 7 per mm. Once more there is ample evidence that the species from the upper mid-waters is the more highly organized and active fish.

Apart from the greater development of the myotomes in *Maurolicus*, there is a striking difference in the nature and composition of the muscle, which may be seen in Text-fig. 43. The drawings are of cross-sections taken just in front of the caudal peduncle. Here the myotomes of *Cyclothone microdon* are formed of one type of large muscle fibre, each with a diameter of about 0·1 mm. *Maurolicus* has two types of muscle fibre. The inner parts of the myotomes consist of fibres with about half the diameter of those of *Cyclothone*, while those forming the outer parts are about half as small again. These latter are presumably red fibres.[1] As the cross-sectional area of the inner parts alone is about equal to the corresponding area of myotomes in *C. microdon*, it will be seen how much finer in texture are the muscles of *Maurolicus*. Study of the density of the fibrils in the muscle fibres of these two species would be of interest.

[1] Red muscle also forms a considerable part of the myotomes of the tunny-like fishes (Kishinouye, 1923), which are the most active of all teleosts.

It will now be clear that the body-tissues of *Cyclothone* are much reduced by comparison with those of *Maurolicus*. A striking indication of the reduced economy of life in *Cyclothone* is (again) found in the form of the kidneys, which have been studied by Owen (1938). One of his drawings is reproduced in Text-fig. 45. The entire system consists of two tubules only, which run side by side down the body-cavity and unite at the bladder. This must surely be one of the simplest kidneys in any adult fish of this size. In *Maurolicus* the kidneys are much more voluminous and have a compact appearance like those of shallow-water teleosts.

These detailed studies of related species may now be used as a guide (see Table 8) to a more general survey of the pelagic fishes living in the upper and lower reaches of the deep-sea. Here the fishes with swimbladders, species belonging to the families Gonostomatidae, Sternoptychidae, Astronesthidae and Myctophidae and having centres of concentration between depths of about 200 and 1000 m. will be compared with those of the groups Lyomeri and Ceratioidea, which have no swimbladder and are most common well below the 1000-m. level.

When these two assemblages are contrasted, the differences between them prove to be very like those between the closely related species that have just been considered. The facts may best be summarized in Table 8. The observations under the Lyomeri and Ceratioidea are based on the work of Nusbaum-Hilarowicz (1923), Bertin (1934) and Tchernavin (1947 *a*, *b*), Waterman (1948), and Bertelsen (1951) and also on personal observation.

A few observations may be added concerning the ceratioid angler fishes. I have looked at females of *Melanocetus murrayi*, *Neoceratias spinifer* and *Danaphryne*. In all three, the first gill-arch is devoid of gill-filaments. Drawings of filaments from the second arch are shown in Text-fig. 46. In *Neoceratias* and *Danaphryne* there are no more than 50–60 gill-filaments in each gill chamber.

Text-fig. 45. Diagrammatic reconstruction of one of the two tubules forming the kidney of *Cyclothone* (after Owen, 1938). (×7·5.) *B*, bladder; *G*, glomerulus; *P*1, *P*2, first and second parts of proximal convolute; *T*, terminal segment.

In the deeper living fishes, every possible economy of tissue has been developed. Compared with the species that live above them and within swimming distance of the productive surface-waters, they seem degenerate. It might be argued that the most trenchant economy has been effected by the evolution of dwarf-males in the Ceratioidea. During the free-living existence it must take much less food to maintain a male than its partner. However, there are other factors to be considered (Bertelsen, 1951).

The ceratioid angler fishes, *Cyclothone* spp., and probably the Lyomeri (*Eurypharynx* has a *leptocephalus* larva), spend their larval life in the plankton-rich surface-waters. Evidently there is not sufficient food of a suitable nature to sustain the larvae at the depths occupied by the adults. However, a good start in life must counterbalance the hazards of this type of life-history.

It is now well-known that the waters below 1000 m. support sparse populations of planktonic animals in comparison with the waters near the surface. The relevant papers and additional evidence

Table 8. *The relative developments of tissue in two assemblages of bathypelagic fishes*

	Gonostomatidae (*most species*), Sternoptychidae, Astronesthes spp. Myctophidae (*most species*)	Lyomeri and Ceratoidea[1]
Vertical range	200–1000 m.	1000–4000 m.
Swimbladder	Present	Absent
Skeleton	Well formed and moderately well ossified	Reduced, particularly in Lyomeri and poorly ossified
Musculature	Well developed	Reduced, particularly in Lyomeri
Eyes	Large	Relatively small (except in certain male ceratioids)
Light organs	Highly developed	Present only on female ceratioids and on tail of Lyomeri
Brain	Large, well developed	Small
Gill-system	Well developed	Much reduced
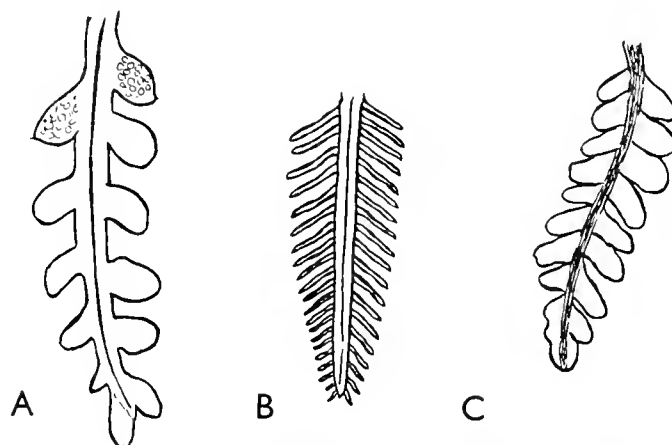
Text-fig. 46. Filaments from the second gill arch of (A) *Neoceratias spinifer*; (B) *Melanocetus murrayi*; (C) *Danaphryne* sp. (A, × 40; B, × 20; C, × 40.)

may be found in Foxton's (1956) paper. Reference to his table 7 will show that in tropical and sub-tropical waters the mean volume of zooplankton between the surface and 150 m. is more than twenty times that between 1000 and 1500 m. In the Kurile-Kamchatka area, the biomass (mg./m.³) of plankton between the surface and 100 m. is about forty times the value measured between 1000 and 2000 m., (and about ninety times greater than that between 2000 and 4000 m.) (Zenkevitch and Birstein, 1956).

Extra data on the biomass of zooplankton in the North-western Pacific are given by Bogorov (1958). In the surface-zone (0–200 m.) the biomass is 1000 mg. m.³ or more, while in the 'transition zone' (200–500 m.), which is generally richer in species than the surface-zone, the biomass falls to about 350 mg./m.³ Below this comes a 'deep-sea zone' (500–6000 m.) in which the biomass varies from 2·64 to 78 mg./m.³ Between 6000 m. and the deep-sea floor the zooplankton-content is less than 1 mg./m.³ Finally some indication of the paucity of life in deeper waters is also given by measurements of the oxygen consumption and phosphate regeneration (Riley, 1951). Over the Atlantic (between 45° N. and 54° S.) the curves of oxygen consumption (ml./l. year) fall sharply below depths ranging from about 250 to 800 m. (see Riley's fig. 25) and Text-fig. 47 of this Report.

[1] The Giganturoidea could also be placed in this assemblage. Nearly all the sizeable specimens in the Dana collections have been taken by nets fishing below a depth of 1000 m., and, apart from their large tubular eyes, they have a low level of tissue development, much like that described under the Lyomeri and Ceratioidea. The giganturoids also have very small kidneys.
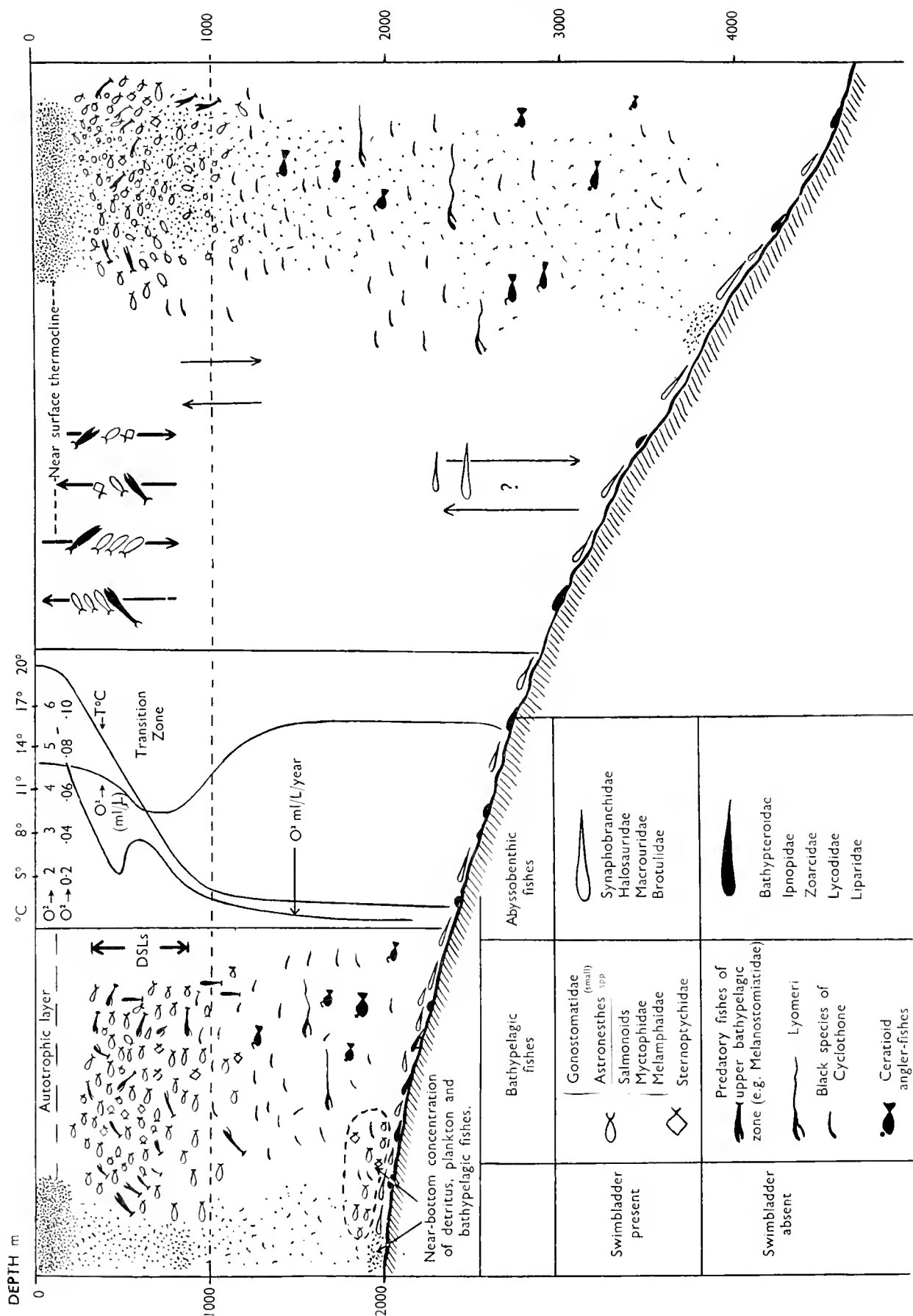
Text-fig. 47. A representation of the vertical disposition of some bathypelagic and abyssal fishes in relation to certain biological and physical conditions, as might obtain in the warmer parts of the North Atlantic. Fishes with a swimbladder have a simple outline, while those without this organ are shown black. The dots from surface to bottom at the left- and right-hand sides of the diagram represent the relative concentration of the zooplankton. Physical conditions are shown in the centre of the figure. Temperature ° C. curve (after Iselin, 1936); oxygen content (ml./l.); oxygen consumption (ml. O₂/l./year), immediately under figures indicating temperature; oxygen consumption (ml. O₂/l./year), calculated from oceanographic data (after Riley, 1951). To the left of these curves of physical conditions is shown the usual daytime depth range of deep-scattering layers, and to the right the differing degrees of diurnal vertical migrations.

Since diurnal migrations are an integral part of the lives of so many fishes existing in the upper oceanic reaches, it is clear that they could not survive and reproduce their kind without drawing on the rich food-supply in the surface-waters. But this feeding-level is beyond the direct reach of the species living below 1000 m. Evidently the most potent environmental stress, against which they have evolved, is the sparse supply of food. But one favourable factor must have been the coolness of their surroundings: the lower the temperature the less the food required for maintaining life (Brown, 1957). On the other hand, at high hydrostatic pressures the pace of life, measured by the rate of oxygen consumption, seems to be increased (p. 90). And, while they do not have to contend with turbulent waters like the fishes that migrate to the surface-mixed layer, the laminar viscosity of the cool seas (5° C. or less) through which they must move is nearly double that at the surface in the warm ocean.

The conclusion is inescapable that the paring-down of the tissues, particularly the reduction of muscle and bone substances, is the most striking of these fishes' adaptations to their living-space. As we have seen, there is every indication that the black *Cyclothones*, ceratioid angler fishes and gulper-eels (Lyomeri) are much less active than the fishes living above them in the upper 1000 m. of the ocean. With the reduction of these tissues they have not only acquired an economy of life to match their food-supply, but have also reduced, more probably eliminated, the effort required to maintain their level in the ocean.[1] If *Gonostoma elongatum*, which also lacks a gas-filled swimbladder, comes close to neutral buoyancy (Denton and Marshall, 1958), this must surely be true of these fishes. In a well-fed *Cyclothone microdon*, the fat stored around the regressed swimbladder, attached to the mesenteries, and deposited in the subcutaneous sinuses must take up more than 10 per cent of the volume of the fish. This light tissue (with a density of about 0·9), together with the reduced muscular tissues and flimsy skeleton, may well make these fishes neutrally buoyant. In a letter to me, dated 8 November 1958, Dr Pérès has recorded his daytime bathyscaphe observations of *Cyclothone*, *Gonostoma* and *Chauliodus*. He writes: 'Ces animaux sont toujours immobiles, paraissant flotter; ils semblent attendre la proie sans la poursuivre, et il m'a été impossible de voirs quelles sont les nageoires dont le mouvement aide à leur equilibre. En revanche les petits *Myctophum* sont presque toujours en mouvement.'

Cyclothone feeds on copepods and chaetognaths (Günther and Deckert, 1953), while Nusbaum-Hilarowicz (1920) found fish-scales and eye-lenses in the gut of *C. braueri*. In three individuals of *C. microdon* taken at St. 395 (48° 26¾′ S., 22° 10′ W. to 48° 26½ S., 22° 06½′ W. 13. v. 1930; N 450 H; 1500–1400 m.), I found the remains of copepods, chaetognaths, euphausiids, together with detrital material and faecal pellets. Female ceratioid angler fishes feed on organisms ranging from copepods to squids and fishes, while in the dwarf, free-living males, copepods, chaetognaths and *Phronima* have been found (Bertelsen, 1951). *Saccopharynx* takes fishes (including benthic species); *Eurypharynx*, crustaceans, worms and fishes (Bertin, 1934). The angler fishes lure their prey and certain species can master fishes several times their own length. Perhaps *Saccopharynx*, which is also a giant swallower, attracts prey by means of the spongy luminous tissue on its wisp of a tail.

Thus all these fishes, including *Cyclothone*, are predatory, and they possess jaws that are adapted for taking a very wide size-range of food organisms. If we again make the same comparisons of species from the upper and lower mid-waters, this adaptation is strikingly revealed.

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[1] Certain of the deeper-living cephalopods (e.g. *Vampyroteuthis*, Cirroteuthidae, *Amphitretus* and other octopods) '…have lost most of their firmness and muscular power. They develop a thick coat of jelly-like subcutaneous tissue and the muscles themselves are sometimes degenerate and invaded by this jelly' (Morton, 1958). This parallel in the most active group of nektonic invertebrates is most striking.

Reference to Text-fig. 43 will show that *C. microdon* has much longer jaws than *Maurolicus,* the suspensoria of which are more or less vertical in position. It is clear that the diet of *Maurolicus* must be restricted, probably to organisms the size of large copepods. However, it lives nearer to good supplies of such food.

Again, *Gonostoma bathyphilum* possesses longer jaws hinged to more backwardly carried suspensoria than its relative *G. denudatum* (see Text-fig. 42). This tendency is carried to an extreme in the Lyomeri in which the suspensoria and jaws are many times longer than the neurocranium. Moreover, the premaxillae and maxillae have been lost, the teeth in the upper part of the mouth being carried on the palatopterygoid elements (Tchernavin, 1947 *a*). The skeleton is also reduced in many other ways. But the most fantastic regression of bone and other tissues occurs in the Monognathidae, fishes that may well live in the same oceanic layers as the Lyomeri (Bertin, 1938).

The jaws, and especially the buccal cavity, of most female ceratioid angler fishes are also large. 'The length of the premaxillary and maxillary is usually more than 50 per cent of the distance from snout to end of cranium and reaches 100–150 per cent in *Caulophryne* and many Linophrynids' (Bertelsen, 1951).

The degree of adaptation of the jaw-mechanisms of these fishes is perfectly evident, a structural emphasis fitting them to an environment with poor supplies of food. In such surroundings it is an advantage to be able to take the largest possible meal that comes along, and at the same time, not to turn aside from a copepod. As Thorson, quoted by Moore (1958) has pointed out, the swallowing capacity of a predator must not only be proportional to the sparseness of the prey, but also be inversely related to its own speed of movement. (Moreover the copepod (or euphausiid) may at least be partly a carnivore and thus be well down the food-chain that begins with the plants of the surface-waters. Bogorov (1958) mentions that deep-sea copepods, such as *Pareuchaeta,* and *Bathycalanus* feed on radiolarians and other small animals. Some deep-sea decapods and amphipods are also carnivores.)

Despite their reduced economy of life, or rather because of it, these fishes are not to be regarded as 'misfits'. *Cyclothone microdon* is perhaps the most ubiquitous fish in the ocean, its range extending from subarctic to antarctic regions, although, the catches of mid-water nets are likely to give a 'false' impression of its abundance owing to its reduced activity. Off Bermuda, Beebe (1937) took eight times as many *Cyclothone* as lantern fishes, but the ocean must support greater numbers, certainly a greater weight, of the latter. (*Cyclothone* spp. are less easily recognized from a bathyscaphe than lantern fishes; thus experienced observers usually see more of the latter.)

Besides the regression of the muscular and skeletal systems, we have seen that the eyes and light-organs of these deeper living fishes are small in comparison with those of the species living above them. I have also implied that this economy of tissue must be linked to reduced development of the nervous and excretory tissues, a correlation which will also apply to the circulatory system. (A study of the alimentary system would also be of interest, for Nusbaum-Hilarowicz (1920) found the intestine of *Cyclothone* to be particularly simple in structure.)

Considering for the moment the eyes, if submarine sunlight is the only controlling factor in their development, the benthic fishes of the abyssal plain would be expected to have markedly regressed visual organs, but this expectation is by no means realized. As Hjort (Murray and Hjort, 1912) wrote: 'But if it be the case that the size of the eyes in pelagic fishes decreases vertically with the decreasing intensity of light, how can we explain the fact that the bottom fishes, like *Macrurus* (= *Nematonurus*) *armatus,* living in abyssal depths possess large and apparently well-developed eyes.' Perhaps this should be called Hjort's Paradox. However, the eyes of the abyssal macrourids and brotulids do tend to be relatively smaller than those of their relatives living over the continental slopes (Marshall,

1954),[1] and in a few species such as *Aphyonus gelatinosus*, the eyes are much reduced. These apparent exceptions will be discussed at a later point (pp. 111–112).

If we compare a black *Cyclothone*, an angler fish or a gulper eel with an abyssal bathypteroid, macrourid or a brotulid, the difference in the relative development of the eyes is not the only contrasting feature. Actually the bathypteroids have small eyes, but their myotomes and skeleton are far better developed, being almost as firm and well-knit as those of their shallow-water relatives, the lizard fishes (Synodontidae). A 3-ft. *Nematonurus armatus* is far better equipped with all manner of tissues than a 3-ft. gulper-eel (and it has kept its swimbladder). The small brotulid *Mixonus caudalis* is similarly 'better off' than a black *Cyclothone* or an angler fish. Many other such contrasts could be made, but here we need only add that the gill-surface of the benthic fishes is far better developed than that in the bathypelagic species.

But the deep-sea floor supports a larger standing crop of animal-life than do the deeper mid-waters of the ocean. In the Kurile-Kamchatka Trench region, which lies under a productive stretch of surface-water, the biomass of bottom-dwelling animals in a square metre was measured at 6·94 g., between depths of 950 and 4070 m. Between 5070 and 7230 m. the quantity fell to 1·22 g. m.[3] (Zenkevitch and Birstein, 1956). Bottom samples taken by a Petersen grab from the 'Galathea' indicate that the deep-sea floor supports an average of ten animals per square metre with a total weight of about 1 g., and this must be a minimum value. Having given these figures, Spärck (1956) concludes thus: 'This surprising density right down to between 5000 and 8000 m. suggests that food conditions in the abyss are not so poor as we have been inclined to think, and this in turn leads us to suppose that abyssal water currents must be stronger than formerly believed.'

The key-organisms in the sediments, perhaps those at the base of the food pyramid, are the bacteria (Zobell, 1954; Zobell and Morita, 1956). They can exist on the dissolved organic matter in seawater and convert intractable substances such as cellulose and chitin into their own substance. The authors just mentioned suggest that the bacteria may be used directly as food, or may aid digestion by living as symbionts in the gut of bottom-dwelling animals. Whatever may be the actual conditions, it is clear that large standing-crops of mud-eating holothurians can exist at depths exceeding 6000 m. (Hansen, 1956). While these animals may be largely free from the attacks of predators, holothurians may still form 30–50 per cent of the biomass of benthic organisms in depths from 3000 to 7000 m., in regions where predatory groups such as the asteroids are particularly abundant (see Zenkevitch, 1954, fig. 2). Finally, at depths down to at least 2500 m., conditions of life at the bottom are favourable enough to attract detachments of active pelagic organisms, such as euphausiids, sergestids and lantern fishes (pp. 87–88).

It would thus seem that there is sufficient food on or near the bottom to satisfy the day-to-day requirements of the relatively highly organized bodies of bathypteroid, macrourid and brotulid fishes. As we have seen, species belonging to the second and third groups have retained a gas-filled swimbladder. There is structural and biological evidence that this organ is functional, even at great depths, but because of its decreased buoyant properties at high pressures some reduction of tissue density is necessary if the animals are to be in hydrostatic equilibrium with their environment. Furthermore, there is evidence that the muscular and skeletal tissues have been somewhat reduced. Even so, the level of development of these and other tissues is much superior to that possessed by the bathypelagic fishes poised above them in the deep, nutrient-poor waters of the ocean. In the endless struggle

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[1] Moreover, *Nematonurus armatus* has a wide depth range (280–4600 m.) extending from regions receiving sunlight to unlit depths. In *Lionurus filicauda*, which seems to be restricted to the abyssal plain (2515–4846 m.), the eyes are proportionately smaller. A 500 mm. *Nematonurus armatus* has orbits measuring 18 mm. in diameter (Nybelin, 1957) while in a 400-mm. *Lionurus filicauda* the eyes are about 10 mm. in diameter.

for a living-space, interaction between fish and environment has been such that tissues have evolved not only to match the biological environment, but to conform to the physical stresses besides.

We are now in a better position to consider the deeper dwelling bathypelagic fishes. Presumably the species of *Cyclothone* once had a gas-filled swimbladder in the adult phase, but this is now only functional during larval life. *Gonostoma bathyphilum* has lost all trace of this organ, but it is well developed in a related species, *G. denudatum*. The ancestors of the ceratioid angler fishes and the gulper eels may also have had a swimbladder.

Now it is clear that the loss of this organ is not related to the pressure factor, or indeed, to any physical effect. The foregoing discussion simply suggests that the cause largely resides in the trophic conditions obtaining in the deeper mid-waters of the ocean. To begin with, a pelagic fish with a swimbladder is able to carry more muscle, attached to a firmer skeleton, than a fish (of comparable dimensions) without such buoyant uplift (Denton and Marshall, 1958). In turn, the proper maintenance and functioning of these tissues require well-developed circulatory, respiratory, alimentary, excretory and nervous systems. But with the loss of the swimbladder, the degree of tissue organization could become 'geared-down' to the low level of potential energy in the biological environment.[1] At the same time neutral buoyancy could be approached or, more likely, achieved.

Moving into the upper thousand metres of the ocean, it is surely significant that most of the plankton feeders, the small gonostomatids, hatchet fishes and lantern fishes possess a swimbladder (Marshall, 1951). Having this internal float, they are able to carry the muscle necessary to propel them upwards during their daily migrations to the food-rich surface-waters. It is also striking that most of the predatory fishes (Stomiatidae, Melanostomiatidae, Chauliodontidae, Idiacanthidae, Malacosteidae and Alepisauroidea) lack a swimbladder. (The exceptions are *Astronesthes* spp. and *Chiasmodon niger*.) We have seen that (pp. 85–86) some of these fishes also undertake vertical migrations. It is probable that they, like *Gonostoma elongatum*, come close to neutral buoyancy through a reduction of skeletal and muscular tissue (Marshall, 1954, 1955; Denton and Marshall, 1958), but the regression of these tissues is by no means so marked as that in the pelagic fishes living in the deep, underlying waters.

Chauliodus sloanei is one of these predators living in the upper mid-waters. The younger individuals live fairly close to the surface and are thus well placed for food (Ege, 1948; Haffner, 1952). The deeper dwelling, older fishes grow to lengths of more than 250 mm.

During the daytime Dr Pérès has watched *Chauliodus* from a bathyscaphe and in a letter dated 17 November 1958 has written of his observations. These fishes hover in the water with the long axis of the body at an acute angle to the horizontal plane, the head being above the tail. At the same time the long second dorsal ray, which is tipped with luminescent tissue (Brauer, 1908), is curved forward over the head so that the extremity of the ray lies in front of the mouth. Clearly, the fish is behaving very much like a female ceratioid and is angling for prey. It is also looking obliquely upward, poised in a good position for detecting prey silhouetted against the down-going and scattered rays of sunlight, but towards sunset, it moves upwards to richer feeding grounds. While the density of its bone and muscle is less than that of a myctophid, it is much the larger fish, and what it lacks in unit muscle-power it gains in size and power of movement, which is also true of most of the other predatory fishes without a swimbladder. Moreover, it is interesting that the only predatory stomiatoids containing this organ are the species of *Astronesthes*, which are smaller than their predatory relatives without it (p. 90). Like its myctophid prey, *Astronesthes niger*, which crosses the upper thermocline during its migrations, has a firm skeleton and compact well-formed myotomes.

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[1] If a teleost had both 'light weight' tissues and a capacious hydrostatic organ it would be overbuoyant.

But Hjort's Paradox is still unresolved. I have mentioned that certain of the brotulids are exceptional in having very regressed eyes. *Aphyonus gelatinosus* is such a species and it lacks a swimbladder. The tissues of its body are also much reduced by comparison with another brotulid of about the same size, *Mixonus laticeps*, a species with a swimbladder. This brotulid has an elongated tapering body, sheathed with scales and equipped with well-knit myotomes. The skeleton is quite firm. The eyes are small, but well-formed, with a wide pupil and a large lens. In the type specimen, which measures 125 mm. in standard length, the horizontal width of the eye-ball is about 4·0 mm.

As indicated by its specific name, *Aphyonus* has a gelatinous appearance. It is semi-transparent and colourless, except for deep-set points of pigment that represent the remains of the eyes. The skin is loose and scaleless, while the skeleton and myotomes are much reduced, the notochord being persistent.

While the type-specimen of *Aphyonus gelatinosus* is bulkier and somewhat longer (standard length 130 mm.) than that of *Mixonus laticeps*, it has a much simpler gill-system. On the first arch there are about fifty filaments with an average length of about 1·5 mm., the second arch bears about forty filaments, while there are only two to three on the fourth arch. *Mixonus laticeps* has somewhat shorter filaments but there are at least a hundred on the first arch and about eighty on the second. Moreover the filaments carry about twenty-five lamellae per millimetre, about twice as many as those developed in *Aphyonus*.

These contrasts are very like those already shown to exist between pelagic fishes from the upper and lower oceanic reaches. Perhaps *Aphyonus* is one of the deeper-living pelagic fishes. This genus, together with *Barathronus*, *Sciadonus* and *Leucochlamys* are placed by Nybelin (1957) in a new subfamily Aphyoninae, '...as they show many mutual similarities and in many respects differ from other Brotulids. As common characteristics may be mentioned a comparatively small body size, a thin loose scaleless skin without or with only very feeble pigmentation, strongly reduced eyes and bone tissues, and a more or less persistent notochord; an opercular spine, characteristic of the typical Brotulids, is lacking.' Moreover, they have very reduced gills and from Nybelin's figures of *Barathronus erikssoni* and *Sciadonus kullenbergi*, it is clear that a swimbladder is absent. As the cleft of the mouth runs obliquely upward in *Barathronus*, Nybelin has suggested that this genus is pelagic in habit. The only direct evidence is the rather young specimen of *Barathronus parfaiti* that was found by Legendre (1934) in the stomach of a long-finned tunny (*Thunnus alalunga*).

I suggest that the entire subfamily consists of deep-dwelling, bathypelagic fishes. If this proves to be so, the common characters might not be indicative of genetic affinity, but rather of convergent adaptation to their food-poor environment. (*Barathronus* and *Sciadomus* are viviparous, while the ovaries of the type of *Aphyonus gelatinosus* contain many eggs, suggesting oviparity.) The deeper mid-waters could even be regarded as a refuge for species that have been edged-out of the two main feeding grounds of the ocean, the waters under the interface between sea and atmosphere and those near the interface between sea and sediments.

If the Aphyoninae are not benthic fishes, the abyssal fauna consists almost entirely of species with small to moderately large eyes.[1] Now Denton and Warren (1957) suggest there are two main factors related to the size and development of the eyes in deep-water fishes. A fish living in the twilight zone is exposed to a large field of light, and here the size of the eye matters less than the relative proportion of the dioptric parts, a wide pupil being necessary. To perceive spots of luminescence efficiently a large collecting pupil is required; the bigger the eye the better. These conditions are met in fishes

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[1] *Typhlonus nasus* is a blind brotulid and might be an exception, but it has a small, thin-walled swimbladder. The bones are soft and flimsy and the myotomes excessively thin. The eyes of *Ipnops* are not regressed but curiously modified. *Leucicorus lusciosus*, which looks more like a bottom-dwelling brotulid, seems to be an exception (see also Marshall, 1954).

from the upper 1000 m., but what of the abyssal species? Their small to moderately large eyes are equipped with wide pupils and large lenses, and they have presumably retained their visual powers because there is luminescent light to be seen (some deep-sea bacteria are luminescent). Furthermore, at least some of them start life in the upper, lighted layers of the sea. (The same is true of the deep-dwelling pelagic species.) A flash of light may mean a euphausiid meal for a *Cyclothone*, or signify a predator. While the eyes of some of these fishes do not properly fulfil the second requirement, they have gone some way to meet it. However, the loss of the eyes in some pelagic fishes, that exist below the 1000-m. level, is compensated for by a marked development of the lateral-line organs on the head. *Aphyonus* has large canals and so has *Ditropichthys storeri*, which may well belong to this fauna (see also Marshall, 1954).

These considerations may seem far removed from swimbladder problems. But they have been set down because I once thought that the regression of the eyes and swimbladder might be linked to the disappearance of the pseudobranch. Myctophids, which have well-developed eyes and swimbladders also have large pseudobranchs. In *Gonostoma bathyphilum* and *Aphyonus gelatinosus*, with small or regressed eyes and no swimbladders, the pseudobranchiae are absent. Now Copeland (1952) found that removal of these organs in *Fundulus* inhibited the inflation of the swimbladder. Furthermore, the blood to the choroidal gland of the eye passes through the pseudobranch in teleosts, although the functional relationship is not clear (Barnett, 1951). However, despite a thorough search under the skin of the gill-chambers of *Astronesthes niger* and *Gonostoma denudatum*, fishes with swimbladders and large eyes, I was unable to find any trace of pseudobranchiae.

We have seen that the loss of the swimbladder in pelagic fishes of the deeper, mid-oceanic waters is not related to the pressure factor, but rather to their harsh biological environment, one that seems to be lacking in the potential energy required to maintain the extra tissues associated with an internal float. Is the regression of the eyes in such fishes as the Aphyoninae, the Monognathidae and *Cyclothone obscura* also to be explained on this basis? Is this a further economy of living tissue?

In dealing with blind cave fishes, Walls (1942) points out that the elimination of the eyes is but a small economy, most of the energy released from food going into motor and secretory activity. However, there is an associated saving of tissue in the central nervous system in the form of a much reduced optic tectum (see Marshall and Thines, 1958). On the other hand, Heuts (1951) maintains that the slow growth-rates, low metabolism and regressed tissues (including the eyes) in *Caecobarbus* are adaptations to the limited food resources of the environment. He goes on to suggest that this is true of all cave fishes. But this is too sweeping a generalization, as Breder (1953) and Cahn (1958) have shown. Some cave fishes, such as *Anoptichthys jordani*, may have good supplies of food and they are most active animals. An *Anoptichthys*, which has a well-developed swimbladder, carries much more muscle than a *Cyclothone microdon* of the same size. Apart from these considerations, caves differ from the deep mid-waters of the ocean in being totally dark.

To return to blind deep-sea fishes, Heuts's concept of the regression of the visual tissues seems more applicable to their case than to the condition found in some cave fishes. While economy in the form of reduced visual and nervous tissue is a small item in the energy balance sheet of an *Anoptichthys*, it might well be critical for an *Aphyonus*. As if to compensate for its loss of vision, *Aphyonus* has a well-developed 'Ferntastsinn' sense in the form of neuromast organs on the head. Do these require less energy to maintain than eyes? At all events, they require smaller centres in the brain. Here the problem may be left with the thought that the food-factor may well be critical, but it may not be the only factor involved.

We are left with certain concepts, which are partly summarized in Text-fig. 47. Living in the ocean at depths above 1000 m. are several hundred species of pelagic plankton-feeding fishes with

well-formed, gas-filled swimbladders. They are muscular, active little fishes with large eyes and brains and highly developed light-organs. Because of the extra propulsive power that a swimbladder allows, they are able to make daily visists to the food-rich, surface-waters, which they must do to maintain their highly organized bodies. Living with them are almost as many predatory fishes, nearly all of which have lost an internal float. In spite of this, these fishes come close to neutral buoyancy by reducing their muscular and skeletal tissues. All have well-formed eyes and brain, and many have complex batteries of light organs. Some of these fishes also migrate to the surface-layers, compensating for their reduced myotomes by increased size of body.

Living below them in the deep mid-waters, are more than a hundred species of pelagic fishes with no swimbladders and very reduced tissues. They are nearly all predatory fishes, many of which lure their prey instead of pursuing it. As they are likely to be neutrally buoyant they can hover in the water without undue effort. The energy balance sheet of these species seems closely fitted to the limited supplies of potential energy around them.

On the abyssal plain, about 250 species of benthic fishes have been taken below a depth of 2000 m. Well over half have well-formed swimbladders and a number of species may range as deeply as 5000 m. Compared with the deeper bathypelagic fishes they are highly organized, but show some reduction of bone and muscle to compensate for the reduced positive buoyancy of a swimbladder at great depths. Most of the species without a swimbladder have an equally good organization, but the food supply seems sufficient to satisfy their day to day requirements.

These differences in form and organization of the tissues are reminiscent of Raunkiaer's (1934) concept of life form in plants.[1] 'All over the world environments varying from place to place determine the existence of different life forms, because the demands of the plants, which are, at any rate, partially expressed by their structure, must of necessity be in harmony with the environment if life is to continue.' Raunkiaer saw that certain structural features were correlated with certain types of environment and that these features were shared by diverse species of plants. Reference to this section, particularly to the table on p. 105, will show that this is also true of the assemblages of fishes that live at the upper and lower levels of the bathypelagic environment. As I hope to continue with this problem, to look more closely at some of the knots in Bigelow's (1930) 'endless web of netting', these few remarks will suffice to conclude this Report.

SUMMARY

Structural development of the swimbladder (pp. 6–50)

Dissection of about ninety species of bathypelagic teleosts has shown that a well-developed, gas-filled swimbladder is present in numerous stomiatoid fishes (most Gonostomatidae, Sternoptychidae, *Astronesthes* spp.); salmonoid fishes (*Opisthoproctus*, *Winteria*) Myctophidae (most species), Melamphaidae (most species) and *Chiasmodon niger* (Chiasmodontidae). The swimbladder regresses during adult life in the Miripinnati, certain of the Stomiatidae and a few Myctophidae and Melamphaidae. It is completely absent in numerous stomiatoids (Melanostomiatidae, Chauliodontidae, Idiacanthidae and Malacosteidae), Alepocephalidae, certain Myctophidae, Scopelosauridae, Alepisauroidea, Giganturoidea, Lyomeri and Ceratioidea.

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[1] Certain continental zoologists have also developed the idea of 'Lebensformtypen' in animals (see Macfadyen, 1957), but the concept is more familiar to botanists.

SWIMBLADDER STRUCTURE AND CLASSIFICATION (pp. 50–58)

The structural plan of the swimbladder has thrown new light on the classification of these groups. The stomiatoids are revealed as a compact (paraphysoclistous)[1] group with a single, bipolar rete mirabile at the posterior end of the swimbladder which has a resorbent capillary bed, obtaining its arterial blood through a by-pass branch of the retial artery. Differences in swimbladder structure may also be useful in distinguishing genera.

The deep-sea salmonoid fishes have a very different (euphysoclistous)[1] form of swimbladder with micro-retia mirabilia supplying the gas-gland. The myctophid swimbladder is also euphysoclistous (with an oval) and three unipolar retia mirabilia enter the anterior end of the sac to carry blood to the three-lobed gas-gland. The families Anoplogastridae, Melamphaidae and Stephanoberycidae (sub-order Anoplogastroidea, Berycomorphi) yet again have a euphysoclistous swimbladder (with an oval) and one or two unipolar retia mirabilia, which run forward from the posterior end of the sac. These and other findings are used to discuss the development of a closed swimbladder in the deep sea, particularly in the predominantly physostomatous[1] Isospondyli, and to consider evolutionary relationships.

THE SWIMBLADDER WALL (pp. 59–65)

The fine structure of the swimbladder wall in bathypelagic teleosts is much like that of other physoclistous groups. Excluding the peritoneal investment, an outer, thin but tough layer of collagen fibres (tunica externa) is separated from the inner epithelial layer by a more voluminous reticulum of fibres developed within a semi-fluid, gelatinous matrix. There is also a layer of smooth muscle fibres near the inner epithelium. Following descriptions of the fine structure of the swimbladder wall in certain species, there is some discussion of its mechanical and gas-proofing qualities. In particular, attention is drawn to the rôle of the submucosa in a swimbladder undergoing compression during a migration into deeper waters. The semi-fluid submucosa would seem to allow the tissues to relax in a uniform manner and the sac to maintain its ellipsoidal shape.

FAT-INVESTED SWIMBLADDERS (pp. 65–68)

In certain bathypelagic fishes (the stomiatoids, *Cyclothone* spp., *Gonostoma elongatum*, *Polyipnus laternatus*, *Borostomias antarcticus*, *Stomias colubrinus*, *S. affinis*, the myctophids, *Lampanyctus leucopsarus*, *Diaphus theta* and the anoplogastroid, *Anoplogaster longidens*), the swimbladder regresses after metamorphosis and becomes invested with fat, which is deposited between the peritoneum and the tunica externa. It is pointed out that this replacement of gas by fat can have but little effect on the 'credit side' of the 'buoyancy balance sheet'.

THE SWIMBLADDER AS A HYDROSTATIC ORGAN AND THE STRUCTURE OF THE GAS-PRODUCING AND RESORBENT PARTS (pp. 68–81)

Like species living nearer the surface or over the continental slope, the volume of the swimbladder in bathypelagic fishes is about 5 per cent of the body volume. It thus functions as a hydrostatic organ, making its possessor weightless in water. But compared to shallow-water species the gas-producing complex (rete mirabile and gas-gland) is highly developed:

1. The product of the number and length of the capillaries forming the retia is high compared to the dimensions of the swimbladder. These two features, together with the form of arrangement of the capillaries, are also considered in relation to the design of the retia as counter-current systems allowing

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[1] See p. 50.

of gaseous exchange between the arterial and venous capillaries. There is evidence that the deeper living species tend to have longer retia.

2. The development of the gas-gland, as expressed by its surface area, is much more pronounced in bathypelagic than in epipelagic species. There appear to be three main types of gas-glands; (*a*) with many giant cells, (*b*) with medium sized cells, and (*c*) with small cells. Intracellular capillaries are found in the first type. Certain cytological features of the gas-gland cells of *Vinciguerria* seem in keeping with the accumulating evidence that the cells actively transport gases from the blood plasma to the lumen of the swimbladder.

The structural features of the resorbent part of the swimbladder, the part by means of which the gas-content can be reduced, are reviewed. Certain aspects of form and function are considered.

The swimbladder and vertical distribution (pp. 82–85)

A well-developed gas-filled swimbladder is only to be found in *bathypelagic* fishes with centres of concentration *above* the 1000-m. level. While numerous other species in the same environment lack such a swimbladder, this condition is universal in bathypelagic species that occur *below* a depth of 1000 m. The loss of the swimbladder in the deeper living species might seem to be related to the pressure factor, to the compressibility of gases and the amounts of energy and gas required to keep the swimbladder inflated at the appropriate buoyant volume against high hydrostatic pressures.

The swimbladder and vertical migrations (pp. 85–95)

Many of the *bathypelagic* fishes living in the upper oceanic reaches (200 to 1000 m.) undertake diurnal vertical migrations. After reviewing the evidence for these movements, the physical and biological background of these migrations is considered. While a number of species cross the near-surface thermocline during their upward migrations, other species are rarely if ever taken in the surface-layers and may be called partial migrators. The physical problems of gas secretion and resorption are considered for both types of migrator. While these fishes are small, active species with a relatively large gill-surface, the provision of enough gas to fill the swimbladder during and after a downward migration seems an immense physiological task unless the gas-gland can store oxygen in a combined form. Concerning the loss of gas during an upward migration, the high ratio between the resorbent surface and the volume of the swimbladder and the very steep concentration gradient between the tensions of the swimbladder gases and those in the blood, may well mean that the rate of gas resorption is high enough to keep pace with the reduction in hydrostatic pressure.

The swimbladder and the economy of life in the deep sea (pp. 95–113)

At least half of the *benthic* species that range below a depth of 2000 m. have well-developed, gas-filled swimbladders, with very long retia mirabilia. Considering also the *bathypelagic* species, there is a direct correlation between the length of the retia and the depth of the living space, a further striking indication of the function of the retia as systems for the counter-current exchange of gases. Apart from implying that the swimbladders of these fishes are functional at great depths (down to 5000 m.) these facts suggest that the loss of the swimbladder in bathypelagic fishes with centres of concentration below the 1000-m. level is not due to the pressure factor. The most potent influence is seen to be the food-poor environment of these fishes, one without the necessary nutriment to support the 'extra' tissues that can be carried at neutral buoyancy by a hydrostatic organ. Compared with the fishes with swimbladders living in the upper reaches (200–1000 m.) of the bathypelagic environment (and with benthic species), the tissues of these deeper living species are much regressed. The life-forms of diverse fishes from these different levels are no less striking than those found in plants.

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PLATE I

Microphotographs of transverse sections through the swimbladder.

Fig. 1. *Vinciguerria nimbaria*; section cut towards the posterior end of the swimbladder between the rete and gas-gland ($\times 150$). Note the artery-vein pairs (each an association of a large and small vessel) running to the gas-gland and the undulating appearance of the fibres in the submucosa.

Fig. 2. Section through the regressed swimbladder of *Cyclothone livida* ($\times 300$). Note the capillaries of the regressed rete mirabile and the regressed cells of the gas-gland (mainly to be seen in the upper right half of the section. See also text fig. 34).

Fig. 3. Section through the rete of *Polyipnus laternatus* ($\times 130$). Note the section cut through the by-pass branch of the retial artery at the top of the photograph.

Fig. 4. Enlarged part of Fig. 3 ($\times 580$). The 'triangle' of nuclei (at about 7 o'clock) in Fig. 3 will be again seen in this figure. The larger capillaries in this section belong to the venous part of the retial circulation.
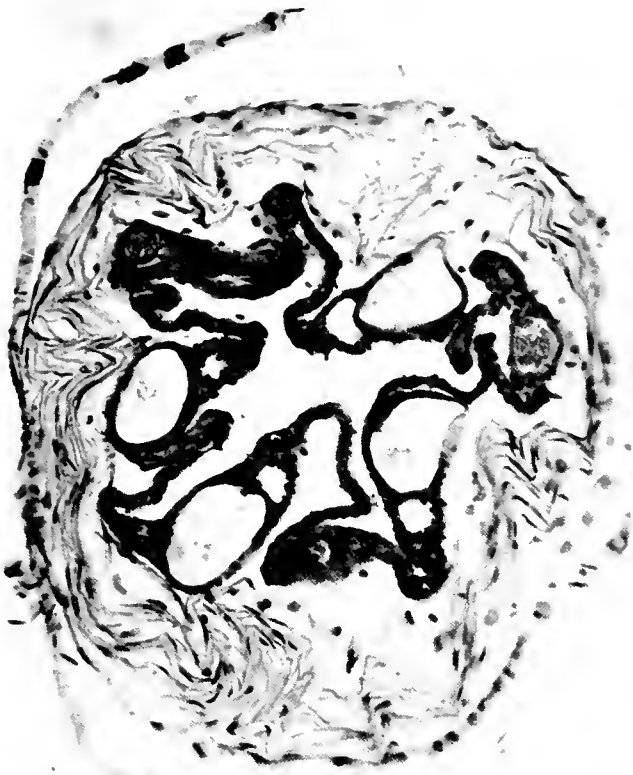
PLATE I

1
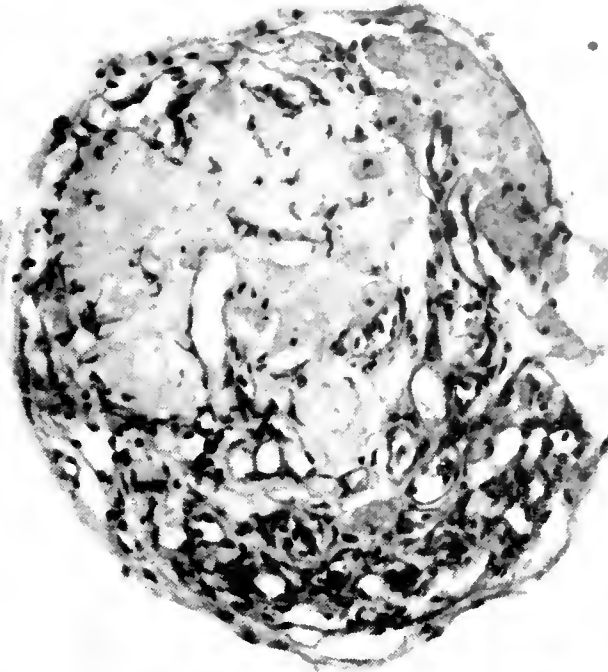
2

3
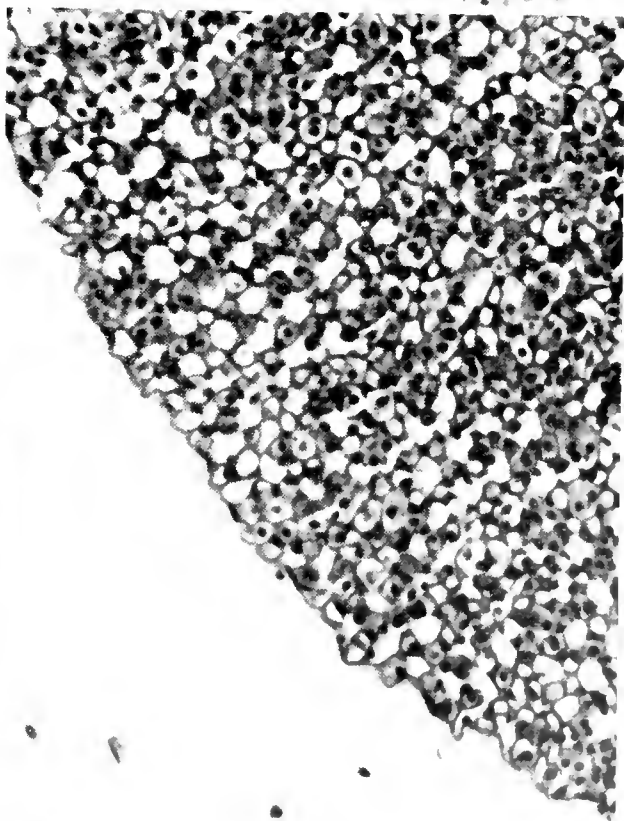
4

PLATE II

Microphotographs of parts of the swimbladder, taken from sections (figs. 1–3, transverse section; fig. 4 longitudinal section).

Fig. 1. Giant cell of gas-gland of *Vinciguerria attenuata* (× 675). Note the intracellular capillaries, surrounded by lighter staining pericapillary cytoplasm and the fine canals joining the capillaries. The vacuolated nature of the pericapillary cytoplasm can also be seen. *b* = base of cell.

Fig. 2. Much enlarged part (× 1500) of a giant gas-gland cell of *Vinciguerria attenuata* to show the vacuolated nature of the cytoplasm surrounding the capillaries.

Fig. 3. Appearance of part of the gas-gland in a compressed swimbladder of *Vinciguerria nimbaria* (× 225). Note the very different shape of the cells from the one shown in fig. 1, which came from a fully expanded swimbladder. The intracellular capillaries and pericapillary cytoplasm (here without vacuoles) may also be seen.

Fig. 4. Entry of a rete into lobe of gas-gland of *Myctophum punctatum* (× 67·5). Note the parallel system of capillaries forming the rete and the capillaries running among the gas-gland cells.
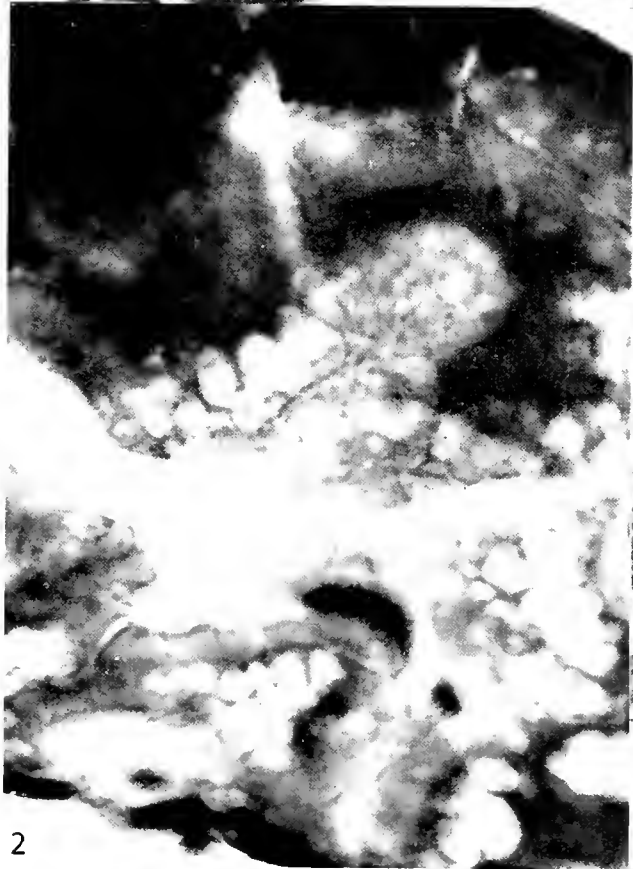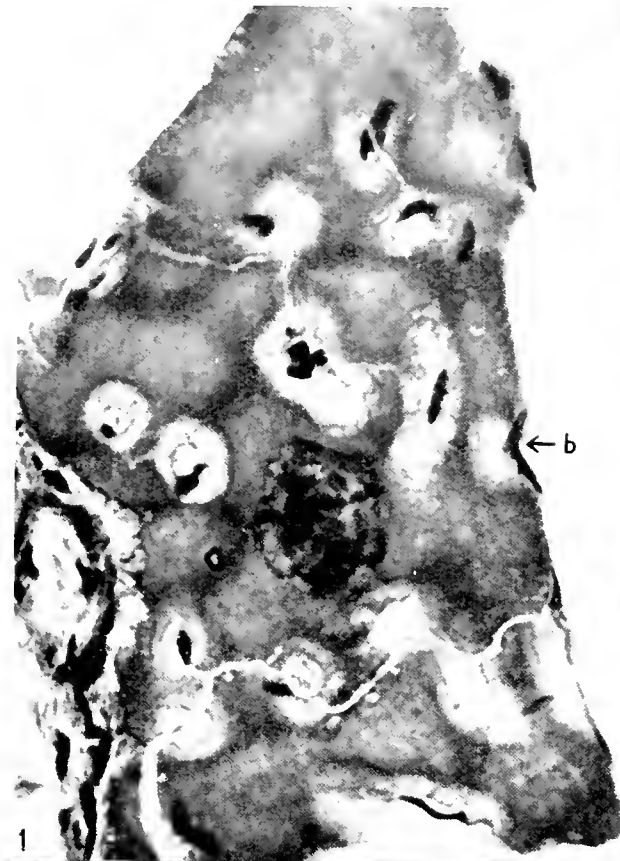
PLATE II

PLATE III

Fig. 1. Microphotograph of longitudinal section of a much contracted oval in the swimbladder of *Myctophum punctatum* (× 120). Note the many blood vessels running through the relaxed tissues of the oval, mostly consisting of the submucosa. The radial muscles of the oval (*rm*) may be clearly seen. An arrow in the main cavity of the swimbladder points to the almost completely closed opening of the oval.

Fig. 2. Radiographs of *Trisopterus minutus* (above) and *Lionurus filicauda* (× 1). Note the very much sharper appearance of the bones of the former.

PLATE III

1

2

DISCOVERY REPORTS

THE BENGUELA CURRENT

by

T. John Hart and Ronald I. Currie

Bostwick H. Ketchum

THE BENGUELA CURRENT

BY

T. JOHN HART AND RONALD I. CURRIE

CONTENTS

THE BENGUELA CURRENT

By T. John Hart and Ronald I. Currie

(Text-figs. 1–96)

INTRODUCTION

WHEN the National Institute of Oceanography took over the ships of the 'Discovery Investigations' in 1949 one of the first objects was to round off some of the work done in the southern hemisphere by the older organization. That research had included a survey of the Peru coastal current, carried out by the R.R.S. 'William Scoresby' in 1931. The late E. R. Gunther, who was in charge of the scientific work at sea, published a valuable report on the results of that survey, which clearly demonstrated the need for further research in such areas. Other duties prevented further work on the data collected from the Peru current prior to the war, and since then much work has been done there by scientists from other countries. The smaller analogous region off South-west Africa on the other hand has received less attention. The 'William Scoresby', however, was recommissioned in 1950 for a voyage to South Africa and the Indian Ocean, and accordingly our new programme, planned in outline by Dr N. A. Mackintosh, allowed for a hydrological and plankton survey of the Benguela current, at first in February–March, and (after subsequent alterations to the ship's programme) again in September–October. There were thus two surveys, the first in the autumn and the second in the spring. They were carried out on similar lines, but within the limits imposed by other items in the programme, of which whale-marking was the most important.

In this report, which aims at providing a general interpretation of the observations made during these two surveys, we apply the name 'Benguela current' to the region of cool upwelled coastal water along the South-west coast of Africa. This water, characterized by a pronounced negative surface temperature anomaly is found mainly between 15° S. and 34° S., and within 100 sea-miles of the coast. Thus it forms only the eastern periphery of the anticyclonic gyral of the South Atlantic, and the adjacent circulation of warmer subtropical water to the westward is excluded. The latter we prefer to speak of as the South-east Trade Wind Drift.[1] This choice of nomenclature, avoiding the application of the name Benguela current to the whole northward flowing limb of the gyral, has arisen from evidence brought together both by Defant (1936) and in the present report, indicating that two distinct current systems are involved, very much as Gunther (1936a) found in the Peru current. Moreover, the name 'Benguela current' is very generally associated with the cold water, so that we hope our restriction of the use of this name to the coastal element will not be misleading, and that it may eventually become generally accepted.

The Benguela current, then, is one of those regions off the western coasts of the continents, where, through the action of the prevailing winds, the effect of the earth's rotation, etc., the cool, nutrient-rich subsurface waters well up to the surface. An intense production of phytoplankton throughout most of the year is promoted thereby, resulting in an abundance of marine life of all kinds.

The rich life of the sea in this region is in striking contrast to the desert or semi-desert conditions that prevail in the adjacent land areas. The cool water along the coast condenses the moisture from the sea-breezes blowing towards the land, in much the same way as if a mountain range intervened, and the coast lying to leeward, in the rain-shadow, as it were, becomes arid and desolate.

[1] Hydrographic Department, 1939.

The abundant marine life of the region contains much which is of value to mankind. Whales, fur-seals, guano islands and potentially rich fisheries are all to be found there. Linked up with these features are areas in the open sea along the coast, with extraordinarily low concentrations of oxygen in the subsurface layers; the bottom deposit of diatomaceous mud is devoid of all but a few highly specialized forms of life capable of existing under almost anaerobic conditions, for sulphuretted hydrogen is evolved through the action of sulphate-reducing bacteria, and locally, under conditions not yet fully understood, this process sometimes increases to such an extent that even the surface waters are affected (Copenhagen, 1934, 1953). This may prove to be one of the factors leading to the recurrent mass mortalities of fish, another peculiar feature usually encountered near the northern limits of the region. Later we shall refer to the lethal effect of oxygen deficiency but it can also reasonably be argued that these mortalities are due more directly to the action of noxious water-bloom, probably of dinoflagellates, since visible discolorations of the sea by super-abundance of living organisms are yet another phenomenon frequently met with, often coincidentally with the mortalities (Brongersma-Sanders, 1948). These mass mortalities and water-bloom formations, which usually take place between midsummer and autumn, seem to link up with seasonal fluctuations in the physical conditions; but the mortalities only assume catastrophic proportions at long intervals, and these show no regular periodicity. Possibly they may follow accentuated deviations from the normal variations in physical factors of the environment, for it will be realized that here again there is close analogy with conditions sometimes encountered off Northern Chile and Peru: the *aguaje* phenomena, the 'Callao painter' or 'el Pintor', and the dreaded 'el Nino' current.[1] Further data bearing on these problems were among our secondary objectives; primarily the surveys were planned to improve our knowledge of the current system as a whole—the norm against which more pronounced local and temporary deviations can be assessed.

Most of the earlier observations from the Benguela current formed but a small part of more extensive programmes as the ships concerned passed down the coast on their way to the Indian Ocean; and more recently, although four of the 'Meteor's' transatlantic profiles traversed the area, they were necessarily carried out at widely separated intervals of time, so that the extent to which they are comparable is limited. Dr Brongersma-Sanders, whose recent work provides an invaluable guide to the literature, has also emphasized the need for more data (1947), and pioneer South African workers in several different fields of research have done the same.

We endeavour to do full justice to previous workers in the next section of this report, but the point has been raised here to show that even such limited observations as could be carried out on a small ship over short periods could still be expected to further the knowledge of the region considerably.

The plan of the surveys consisted of three main lines of full 'stations' (off Walvis Bay, Sylvia Hill, and the Orange river) worked east and west, that is, nearly normal to the coast and to the main trend of the isotherms; and four lines of intermediate or subsidiary stations, the first in the northern part of the area east and west, the second south-westward out to the offshore end of the first line of full stations, and from the inshore end of each line of full stations to the offshore end of the next. The east and west lines were disposed almost on the same latitudes as the eastern portions of previous 'Meteor' profiles, and thus afforded some direct comparison with previous work. Positions of all the stations and the 200 m. depth contour are shown in Figs. 1, 2 and 4 (pp. 143 and 146).

During the first survey (Fig. 1), we endeavoured to work the outermost station on each east-west line in oceanic depths beyond the continental slope, and the spacing of subsequent stations was therefore determined partly by the width of the shelf in the longitudes chosen and partly by practical

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[1] Hitherto known by this name in oceanographical literature, Schweigger (1949) has recently challenged the correctness of this usage.

considerations. In general they were from 10–25 sea-miles apart. At full stations complete series of water-samples with temperature determinations at standard depths throughout the water-column were obtained; simultaneously standard series of vertical-closing plankton nets were fished down to 1000 m., or as deep as soundings permitted, and a vertical haul with the fine-meshed phytoplankton net was made. Towed plankton nets were not fished during the first survey owing to lack of time. Full details are given in the Station list (see references).

At the intermediate stations the ship was hove-to for a vertical haul with the phytoplankton net, which enabled us to make temperature observations with the bathythermograph loaned by the U.S. Navy, down to the limit of the depth range of the instrument (138 m.). Three hauls with a commercial otter-trawl (WS 974, 990, 999) were made on the continental shelf, providing some indication of the nature of the demersal fish-fauna and material for speciation studies in the genus *Merluccius* (hake) by Mr N. B. Marshall of the British Museum (Natural History).

Seventeen full stations and twenty-two intermediate stations were worked, over the area of some 60,000 square miles, in nine days. We could not spend more time in order to make the coverage more complete, since this could only have been done at the expense of the rest of the ship's programme. Details of the itinerary are given below (pp. 141–144).

The second survey (Fig. 2) was essentially a repetition of the first, at the opposite season of the year, but with more time available it became possible to increase the collections at the reoccupied stations, and to make some additional observations. Oblique and horizontal towed plankton-nets were fished at all full stations in addition to the vertical series, and horizontal towed nets at intermediate stations. Bottom samples were collected at nearly all the stations on the shelf, and a few additional stations were occupied for this purpose alone, to gain further knowledge of the distribution of the diatomaceous 'azoic' mud. The ship also worked in collaboration with Commander W. J. Copenhagen for a brief period while in the Walvis Bay area, assisting in researches he has described in another report (Copenhagen, 1953). Additional intermediate stations were worked both north and south of the area previously covered, and alternate stations on the most northerly, east–west line were made into full stations. Thus the number of full stations was increased to twenty and of intermediate stations to forty-four (thirteen being bottom-sampling stations only).

Full details of meteorological, physical and chemical data collected, and biological collecting gear used at each station on both surveys, are given in the Station List, already published in the Discovery Reports (1953). Methods are described and discussed in a later section of this report.

The ship was commanded by Lieut.-Cmdr A. F. Macfie, O.B.E., R.D., R.N.R., whose experience and ready assistance with the work at sea, and advice to the scientists when practical considerations rendered modifications of programme unavoidable, were prime factors in the successful completion of both surveys. Mr R. Baty, the chief Engineer, and his department gave unstinted help in servicing scientific gear, despite unlooked for difficulties with other auxiliary machinery. Mr K. Maclean, the chief officer, who organized the assistance needed from the watch on deck during station work, also obtained valuable recorder runs with the echo-sounding machine, and with the bo'sun, Mr Yorke, devoted much care to its maintenance. Mr M. R. B. Hawkins, the navigator, also recorded meteorological data, and Mr W. Slater, third officer and trawling expert, also helped in many ways outside his routine duties. Such projects must always depend upon the able co-operation of the whole ship's company, so that the data recorded and the biological collections made are a reflection of the way all hands turned to at an arduous, unfamiliar assignment.

The scientific personnel were Dr T. J. Hart, Dr (then Mr) Robert Clarke and Mr R. I. Currie. Dr Hart was in charge of the work at sea during the first survey, handing over to Dr Clarke at the Cape

as previously arranged. Dr Clarke's judgement in making additional observations during the second survey, when more time unexpectedly became available, greatly increased its value. Owing to his preoccupation with whaling research he has not participated directly in the writing of this report. In preparing the account of the second survey we have frequently made use of his journal. That the field work owed much to his efforts throughout should be obvious. All chemical estimations made at sea were carried out by Mr Currie.

We are particularly indebted to the Director of the Marine Biological Association's Plymouth Laboratory and his staff for unrivalled working facilities before the new premises of the National Institute were available, for much fruitful discussion and for practical help. By arrangement with Dr G. A. Steven, Skipper W. H. Crease with his crew of the R.V. 'Sula', and the M.B. 'Gammarus', gave much help while the ship was in Plymouth on her outward voyage, and again on her return.

All our colleagues on the staff of the National Institute have assisted the work in some measure, but special thanks are due to Dr G. E. R. Deacon and Dr N. A. Mackintosh for their valuable advice and encouragement during the preparation of this report, to Dr H. F. P. Herdman for the care and attention he devoted to the scientific equipment of the ship before sailing, and to Miss D. M. E. Wilson for assistance in computing of values and checking data for the station list.

The assistance of the naval authorities who 'mothered' the ship when she called at Devonport, Gibraltar, Freetown and Simonstown, extended down to the provision of odd spares for what must have seemed to them some very odd gear, and was, of course, absolutely essential to the successful completion of this part of the programme.

We also wish to record our thanks to the Director of the Naval Weather Bureau for providing relevant meteorological data; to Cmdr C. E. N. Frankcom, O.B.E., R.N.R., of the Marine Division, Meteorological Office, and to Mr E. W. Barlow of his staff for data on surface drift and much helpful discussion.

Dr J. H. Oliver assisted greatly in devising a suitably robust instrument for carrying out our phosphate determinations and by providing laboratory facilities in London before the ship sailed. Dr K. R. Butlin, of D.S.I.R., assisted by confirming the presence of sulphate-reducing bacteria in the bottom-sample from St. WS 1074.

Many people in the Union of South Africa befriended the ship, both officially and personally. Among those who helped more particularly with our Benguela current problems were: Dr C. von Bonde, then Director of the Fisheries Survey Division, Department of Commerce and Industries, and his staff, who gave us laboratory facilities and opportunities for discussion on many topics of common interest. The Head of the South African Weather Bureau provided most valuable data. Commander W. J. Copenhagen, with whom we have discussed plankton production and the 'Walvis Bay problem' over many years, introduced us to Dr Liebrandt, Director of Chemical Services, Department of Agriculture, who provided chemical laboratory facilities on this occasion. Dr S. P. Jackson of the Geography Department, University of Witwatersrand, gave most valuable advice on the meteorological factors involved, as did Professor J. H. Day of Cape Town University on zoological matters. Dr J. H. Maconnell of Walvis Bay, supplied some first-hand local information on the fish mortalities.

PREVIOUS WORK

EARLY VOYAGES

West African exploration received its greatest initial impetus in the latter half of the fifteenth century. Continuing their pursuit of the Moors, the Portuguese initiated a series of somewhat warlike exploratory voyages down the West African coast. Attempts to sail southward were for a long time

defeated by a great reef off Cape Bojador, but this was eventually passed in 1433 or 1434, and further voyages became more and more directed towards trading and colonization. King John commissioned an esquire of his country, Diego Cao, to continue further exploration into the Gulf of Guinea, and on his second voyage in 1484–6 Diego Cao penetrated southward beyond the mouth of the river Congo (Ravenstein, 1900).

It was the custom of the Portuguese at this time to set up marble pillars surmounted by a cross, with which to mark their achievements. These pillars, or 'padraos', had been introduced to replace wooden crosses which were used before but found to rot away too quickly. Diego Cao carried several of those padraos with him, constructed and suitably inscribed, before leaving Portugal. He set up one at the most southerly point which he reached, naming it 'Cabos do Padraos'. It is now known as Cape Cross. It seems that Cao sailed rather further south than this, to about 22° 09' S., before he returned to the north.

Interesting to note is a remark by Ravenstein (1900) on Martellus's chart, which documented the discoveries of this period. He says, 'To the south of it [Cape Cross] on Martellus' chart, we notice a Praia dos Sardinhas (sardine shore), now known as Sierra Bay...'. The position of this shore coincides with the region where we now know that extensive mortalities of fish occur. It is possible, therefore, that Diego Cao had observed such a mortality of sardines.

Diego Cao appears to have died on the return voyage, and the exploratory work was taken over by Bartholomeu Diaz. Diaz left Portugal in 1487 and was the first to succeed in rounding the Cape of Good Hope. He set up a padrao at Luderitz Bay (Diaz Point) and another at the Cape. The final linking up of the trade route to the east was accomplished by Vasco da Gama (1497–9) (Ravenstein, 1898). One might conjecture that da Gama had benefited from the experience of his predecessors for on his way to the Cape he stood well out to sea and first touched the South African coast at St Helena Bay. In so doing he would have avoided the greater part of the contrary currents and winds of this coast, and would have been able to tack into the trade wind, but there is, of course, no proof that it was these considerations that led him to adopt such a route.

Although the early Portuguese place-names are very descriptive and tell us a lot about their observations, no detailed records of these voyages have been found. Several expeditions visited this coast in the following centuries, principally in search of guano and further inland exploration, but not until the nineteenth century have we been able to find any records of meteorological and hydrographical observations.

PREVIOUS SCIENTIFIC OBSERVATIONS

In 1820 Major James Rennell summed up the existing knowledge of the ocean currents' and this work was published posthumously in 1832. With regard to the currents of the South-west African coast he remarks (pp. 119 et seq.):

But we have no detailed accounts of the circumstances of the currents along-shore, between the parallels of 28° and $11\frac{1}{2}$° south, although the existence of such is well known; so that the continuity of the thread of current is never broken between that in the Indian Sea and the Equatorial current. The first notice, from authority, of a current hereabout, is its issuing from the deep recess of the coast of Benguela, between $9\frac{1}{2}$° and 11° S., in a W.N.W. and N.W. by W. direction, (as if the water had been forced in there) and with a rate of 14 to 25 and 30 miles per day.

From the just mentioned Bay of Benguela the current ranges along the coast to the N.W. receiving the waters of the Zahir or Congo River, the outfall of whose waters runs nearly in the same direction with the sea current, that is N.W., and only marks its character by the increased velocity of the stream, and the lowering of its temperature.

While commenting thus on the coastal currents, Rennell was well aware of the more definite drift produced by the trade wind farther from the coast. This he called the South Atlantic current.

The generally accepted theory that the cold current along the coast was a direct flow from high southern latitudes was held until the middle of the nineteenth century, although Rennell recognized a continuity in the surface drift from the Indian Ocean to the Atlantic, around the Cape of Good Hope. Sir James Clark Ross (1847) on his passage to the Antarctic carried out a series of temperature measurements around the Cape, which show conclusively that the cold water on the west coast was an isolated phenomenon, and was not continuous to the south. Whilst approaching the African Coast in the vicinity of Paternoster Point on the 8 March 1840, he remarks:

By 1 p.m. the next day the temperature of the sea had fallen from 70° to 56·5° F., that of the air being 65° and the mist unpleasantly cold to our feelings. We were at this time in 32° 21′ S., 17° 06′ E., therefore about 45 miles from Paternoster Point, when we struck soundings in 127 fathoms on a bed of fine dark sand. We had expected to have found an elevation in the temperature both of the air and sea on our approach to the African coast, by reason of the heat radiation from its shores; but the cause of the depression became evident on the morning of the 9th, when having sighted Cape Paternoster at daylight, we found we had to contend against a current increasing in strength and coldness of temperature as we neared the land.

Ross had to spend several days beating up to the Cape, and while doing so he took the opportunity of making observations of temperature at different depths and distances from the land. These he has tabulated, and from them he concludes:

All these circumstances combine to show that a northerly current of very limited extent, but of considerable force exists from the Cape of Good Hope, along the western coast of Africa; which in general terms, may be represented by a volume of water sixty miles wide and two hundred fathoms deep, averaging a velocity of one mile per hour, and of the mean temperature of the ocean, running between the shores of Africa and the waters of the adjacent sea. The cloud of mist which hangs over this stream of cold water is occasioned, of course, by the condensation of the vapour of the superincumbent atmosphere, whose temperature is generally so many degrees higher than that of the sea. It is sufficiently well defined to afford useful notice to seamen of their near approach to the land.

After leaving Simon's Town, Ross continued his temperature measurements, and

found the temperature of the surface of the sea to increase rapidly after leaving Cape Point,...showing that we had got to the southward of the cold water current that runs along the west and perhaps the south coast of Africa.

It is evident therefore that this current does not come down directly from the south, as it only extends to seven or eight miles from the Cape and beyond that distance we have to descend to over six hundred fathoms to find water of so low a temperature.

These observations do not appear to have received very wide attention, for even up to 1910 (Engeler), some authors upheld the continuity between the West Wind Drift and the cold current on the west coast of South Africa. Findlay (1874), Bourke (1878) and Galton (1883) all speak of a south polar current on this coast, although Bourke appears to have been mystified by the patchy distribution of the cold water. 'But the most remarkable feature of this N.W. current from the Cape of Good Hope is the sudden manner in which its cold waters simultaneously appear along the land to the northward of Cape Frio.'

The origin of the cool water by upwelling was inferred both theoretically and by comparison with other regions by Witte (1880), Buchan (1895) and Schott (1902). It was finally confirmed by the serial oceanographical observations of S. M. S. 'Möwe' (Schott, Schulz and Perlewitz, 1914).

Many early writers on the region make general references to its great wealth of marine life. Pechuël-Loesche (1882, p. 283) writes of 'a species of herring *Pellona africana* that presses shorewards from the South Atlantic current in immense shoals, from November to February'. Though most of his observations were made far to the north, where the upwelling is a much more seasonal phenomenon than in the region off South-west Africa, the analogy with the behaviour of other clupeoids farther south is most striking. Pechuël-Loesche also appears to be responsible for the present name of the current.

As we have said, Rennell (1832) applied the name 'South Atlantic current' to the more definite drift of the trade wind offshore. Later, Findlay (1867) called the current the 'South African current', a name also used by Dankleman (1878). This name referred to the whole water movement off the west coast of South Africa, and this again was termed the 'Sud-atlantische Strömung' by Pechuël-Loesche (1882). In a later paper, however, cited by Schott (1931), Pechuël-Loesche uses the name 'Benguela-strömung'. The *Africa Pilot*, Part II, 1939, distinguishes two current systems, the South-east Trade Wind Drift, and the Benguela current inshore, and as stated previously we have chosen to follow this nomenclature throughout this paper.

Of the more recent expeditions to the South-west African region, that of the *Valdivia* has contributed most to our knowledge of the biology of the region. The majority of their stations lay further from the coast than we could have wished, but nevertheless their observations have helped to lay a basis for later work. In collating these observations Schott (1902) was able to summarize the existing data on the physical phenomena of the region, but of all the 'Valdivia's' work that part which has been of most service to our present investigations is the great advance in the taxonomy of many of the southern subtropical organisms which resulted from her collections in adjacent waters. Karsten's report on the phytoplankton (1906), which quotes from Schimper's field notes, has been a constant help in working up the microplankton.

The voyage of S.M.S. 'Möwe' in 1911 was more strictly concerned with surveying the coastal regions, and some valuable physical and chemical data were collected. Evidently no biological observations were made. The physical data have been dealt with by Schott, Schultz and Perlewitz (1914) and later by Franz (1920, 1921) who considered at length the seasonal fluctuations of the current.

Our knowledge hitherto of the oceanographical phenomena of the region is, however, based principally on the extensive work of the Deutsche Atlantische Expedition 'Meteor'. The data collected by the 'Meteor' enabled Defant (1936) to investigate the mechanism of the current system, while numerous papers, among which Hentschel's work is outstanding, have provided an understanding of the general biology of the region. The 'Meteor's' work will be referred to later (p. 134).

Systematic collecting by the vessels of the Discovery Committee, which in these waters was mostly during the winter months and off the southern part of the South-west African coast, has aided the identification of our material, and has also been a guide to the extent to which species found in abundance in the Benguela current are peculiar to that region, or are merely local concentrations of wide-ranging oceanic forms. In this way both Hendey's report (1937) on the Plankton Diatoms of the Southern Seas, and John's report (1936) on the southern species of the genus *Euphausia*, help in the interpretation of the 'William Scoresby's' collections.

Much pioneer work has been carried out by the South African Division of Fisheries and Marine Biological Survey under the direction of Dr J. C. F. Gilchrist and latterly by Dr C. von Bonde and his successors. Dr K. H. Barnard of the South African Museum has been particularly active among the many specialists working upon this material, and although the collections rarely extended north of the Orange river, they form the basis of our knowledge of many species extending farther north. Boden's account (1950) of the coastal plankton diatoms from Cape Peninsula to Lambert's Bay has been a constant help.

Work on analogous conditions elsewhere has, of course, advanced our knowledge of the basic physical and biological factors important in upwelling regions. Schott's work (1902, 1931, 1942, 1951) on the Peru current and upwelling regions generally, has done much to show how closely analogous the different upwelling regions are. Gunther's account (1936) of the work of the 'William Scoresby' in the Peru current, gives details of the current pattern, mortality phenomena and discoloration of the sea, all of which are closely mirrored in the Benguela data.

Perhaps the best known of all upwelling regions, owing to its ready accessibility, is the Californian current. Abundant recent researches into its oceanography carried out by various leading workers show essentially similar relationships to those which we have found in the Benguela current. The numerous references in later sections should show how valuable this work has been in interpreting the present data.

One feature of the Benguela current region which has attracted widespread interest is the occurrence of fish mortalities, particularly in the vicinity of Walvis Bay, and their possible causes, biological or otherwise. The whole subject has been comprehensively discussed by Dr Brongersma-Sanders (1948) who treats all the relevant literature thoroughly. This and further recent work, in particular some of the results of the Danish 'Galathea' Expedition (1950–2), will be discussed in the appropriate sections.

The work of the 'Meteor' expedition

The extensive data collected by the 'Meteor' in 1925–7 have revealed the general pattern of the circulation in the South Atlantic (Wüst, 1950) and the disposition of the observations was such that some of them fell within the South-west African region. This enabled Defant (1936) to present the most complete account of the region so far.

The 'Meteor' observations consisted of several more or less latitudinal lines of stations across the Atlantic Ocean. The eastern ends of five of those great sections fell within the Benguela current, and it is those stations which Defant used. Defant supplemented his study of the 'Meteor' observations by a new analysis of the Dutch surface current observations. These he meaned in one degree areas (one degree of latitude by one degree of longitude) for each quarter of the year, and his results (Fig. 6) present us with an interesting new interpretation of the surface water-movements. The outstanding feature of these current charts is that they reveal a one-sided line of divergence. It lies·in a N.N.W. direction along the coast, from about 20° to 30° S. In the south it is about 160 sea-miles from the coast, and in the north 300–350 sea-miles. To the west of this line the current sets to the west, but to the east of it the current runs more or less parallel to the divergence but is somewhat irregular on its coastal boundary.

Comparing this system with the iso-anomaly lines of surface temperature (the lines of equal difference from the latitudinal mean) Defant further finds that the region of strongest negative anomaly, the coldest water, is confined to the coastal current, and is most marked in the region between 23° and 31° S. where the divergence is also most pronounced.

The vertical thermo-haline distribution on the five 'Meteor' 'Profils' shows a correspondingly good agreement with the surface picture. 'Profil' IV in 34° S. shows but little evidence of upwelling close against the land, while on 'Profils' II ($28\frac{1}{2}°$ S.) and VII (22° S.) the characteristic uplift of the isotherms and isohalines against the coast indicates the upwelling of the subsurface-waters from a depth of about 300 m. The more northerly 'profils' suggest a sinking rather than an uplift of water against the coast. In 'Profil' VI (15–16° S.) the isotherms and isohalines, at a depth of 30–40 m., descend toward the coast, and in 'Profil' VIII (9° S.) this is even more pronounced. Thus the region of most intense upwelling, as adduced from the vertical pictures, corresponds with the position of the most marked negative surface temperature anomaly and the most well-defined divergence in the surface currents.

Defant then considers theoretically the problem of the circulation by examining the effect of winds on two bodies of water of different density lying in a canal. This will be discussed in more detail later, but for the present it will suffice to say that by applying his derived theory to the South-west African waters, he concludes that outside the divergence there must be a vertical eddy in the upper layers. Below the axis of this eddy the water will move towards the east, ascending to the surface inside the

divergence line and producing in the coastal waters a distribution of density such that a current will form parallel to the coast. Seawards of the divergence line, and in the upper part of the vertical eddy, the water will be transported offshore.

Studying the general biology of the region, Hentschel (1936) found it necessary to adopt some arbitrary spatial definitions of the several sea areas he discussed. The 'ten degree field' extending westwards as far as St Helena which he took as his Benguela current region has unfortunately masked the great richness of the coastal current inshore. Consequently most of the generalizations he felt able to make apply rather to the subtropical oceanic surface water. Of the existence of the rich coastal belt he was, of course, very well aware. This was the only part of the region where large quantities of diatoms were to be found among the microplankton. He did not, however, regard the coastal current as distinct from the oceanic circulation, whereas our present results indicate that the natural boundary between the two types of surface-water is more significant than any of the boundaries of his arbitrarily chosen areas. No doubt he was unable to demonstrate the effect of this natural boundary on account of the wide spacing of the 'Meteor' stations, and the fact that the physical data were only partly digested by the time his work was published. His reference to the characterization of the region by the steep east–west gradient in microplankton quantities rather than by an abrupt transition such as our results indicate, his inclusion of many warm-water forms among the characteristic dominants of the region, and his insistence on the dominance of Dinophyceae over Diatoms among the protophyta, all arise from the same causes. Provided this is all borne in mind it can be seen that his generalizations are in very good agreement with our own findings—that is, apart from his insistence on the importance of the 'South-west Africa Tongue' which will be discussed later.

While extremely valuable for interpreting the large-scale picture, the 'Meteor's' observations unavoidably had the disadvantage of being widely spaced both in time and geographically, and the 'William Scoresby' surveys can be considered as the next logical step in making a more localized and intensive study of the Benguela region in particular.

METHODS USED IN THE 'WILLIAM SCORESBY'

OBSERVATIONS AND COLLECTIONS

Throughout the two surveys the watch-keeping officers maintained regular meteorological observations. In addition to those kept at four-hourly intervals, further records were taken while the ship was occupied on 'station'. The observations included personal estimates of the force and direction of wind, sea and swell, and instrumental records of barometric height, and dry- and wet-bulb temperature.

Continuous echo-soundings were made whenever possible, but these were restricted to the continental shelf and slope, as the depth range of the machine (720 fathoms, 1317 m.) did not permit any deep-water sounding. The latter were eventually obtained by a Lucas wire-sounding machine, but unfortunately this was not functional during the first survey. On the second survey, however, the Lucas machine made it possible not only to obtain deep soundings but also to delimit the extent of a region of reducing mud on the sea floor. For this the sampling technique depended upon the nature of the sediment, and both Baillie rods and snapper leads were found effective. The samples were preserved in alcohol after a preliminary examination.

The 'William Scoresby' was fitted with a distant-reading thermograph which provided a continuous record of the sea temperature. Since the bulb of this instrument was installed in the engine condenser intake, the record represents the temperature at a depth of about 4 m., but this of course varied considerably with the degree of loading of the ship. Checks on the accuracy of the instrument

were made frequently by comparison with insulating water-bottle measurements, and showed no significant deviation from the original calibration.

It was decided while planning the surveys that intermediate observations of temperature between the lines of full stations would be invaluable in constructing a detailed picture of the upper layer circulation. For this a bathythermograph was used. The instrument, the standard U.S. Navy pattern manufactured by Wallace and Tiernan Prod. Inc., New Jersey, conformed to the specifications of accuracy prescribed by the makers. (Temperature $\pm 0.1°$ F. and pressure $\pm 4\frac{1}{2}$ ft. with a depth limit of 450 ft.) Frequent calibrations of both temperature and pressure elements indicated a remarkable constancy, and no correction of the results has been necessary.

All water-samples were taken by standard methods, at the depths recommended by the Association Internationale d'Océanographie Physique. The Nansen–Pettersson insulating water-bottle was used for sampling the shallower depths, as a rule not over 400 m., but on certain occasions it was operated to a depth of 600 m. when an additional reversing hoist could be omitted thereby. At greater depths Munro-Ekman reversing water-bottles were employed. Three of the latter were used in each hoist, and while all carried two protected reversing thermometers, the upper and lower bottles were equipped with unprotected reversing thermometers as well.

Biological collecting during the surveys was mainly confined to standard series of plankton net hauls. The nets used and method of fishing were similar to those employed during the pre-war work of the Discovery Investigations (Kemp, Hardy and Mackintosh, 1929). The vertical series at full stations in oceanic waters included hauls with the Nansen pattern closing net, 70 cm. diameter at the mouth (N 70 V), at depth intervals of 50–0 m., 100–50, 250–100, 500–250, 750–500 and 1000–750 m. At shallow water stations the series was modified so as to work as close to the bottom as possible. A 100–0 m. vertical haul with the N 50 V phytoplankton net was also made. During the second survey oblique hauls were made with the 1-m. stramin net (N 100 B) and 70 cm. silk tow-net (N 70 B) on 200 m. of warp, maximum depth being recorded by Kelvin tube, and a 1-m. net (N 100 H) was also towed horizontally at the same time. These were in addition to the vertical series. Towed nets were not used during the first survey. In addition to the hauls at full stations, the N 50 V was worked at all the intermediate bathythermograph stations on both surveys.

A full-sized commercial otter-trawl (OTC) and conical dredge (DC) were used at a few stations on the shelf during the first survey, and during the second, numerous bottom-samples were collected with snapper-lead and Baillie rod. Full details of dates, times, etc., at which these types of gear were used are given in the Station List (1953) which also includes full definitions of the standard abbreviations employed.

The centrifuging of water-samples was not employed as a routine method for phytoplankton sampling, but was used for provisional identifications of dominant organisms in areas of discoloured water, whence surface-samples were preserved for subsequent analysis.

It was important above all to extend the basic physical and chemical observations over the widest possible area, and it was mainly for this reason that we did not attempt more comprehensive work on the phytoplankton, and more particularly on the smaller organisms known to escape nets. The Harvey method of pigment extraction from the catch of a fine-meshed vertical net fitted with a flow-meter (Harvey, 1934), which had proved most useful in the antarctic zone (Hart, 1942) was not used because it was already known from the 'Meteor' results (Hentschel, 1936) first, that dinoflagellates were of vastly greater relative importance in this area than in the antarctic, and their mixed pigments tend to vitiate direct visual colour match; secondly, that the nanno-plankton forms would similarly be of greater relative importance here. In the event, we found diatoms so numerous in the rich coastal belt that the earlier form of Harvey's method would most certainly have yielded valuable results. More

recent refinements of the pigment extraction method successively developed by Riley (1938), Krey (1939) and Richards and Thompson (1952), should certainly prove a most valuable line of investigation in the Benguela current area.

ESTIMATION OF SALINITY AND PHOSPHORUS

The confined laboratory accommodation on board the 'William Scoresby' made it necessary to restrict as much as possible the amount of analysis carried out in the ship. Estimations of at least salinity, phosphate and oxygen were desirable for the work. Of these properties the salinity is by far the most stable, and unaffected by normal storage, and it was decided to keep the salinity samples for later analysis on shore. This has been the practice in the past on board the 'William Scoresby'. The estimations were eventually made by the Government Laboratory, London, to whom we owe our thanks.

The Atkins–Denigès colorimetric method was used for the determination of the dissolved inorganic phosphate-phosphorus. Recently, many new photometric systems have been described, which facilitate the colour comparison and attain a high standard of accuracy, but after experimentation both before the cruise and later on board the ship, it was decided that in the conditions in which we worked a visual comparison would yield the most satisfactory results of the required degree of accuracy. This method was adopted and we are greatly indebted to Dr J. H. Oliver for perfecting a suitable instrument for the purpose.

A Lovibond type of colorimeter was used. This had a series of thirty-three specially made glass slides, with colours flashed on to them representing a range in phosphate concentration from 0·03 to 3·00 mg. atoms $P/m.^3$ The slides were calibrated by the same operator in a shore laboratory, against standard phosphate solutions (KH_2PO_4) made up in phosphate-free sea-water. (This latter, of salinity 35·00‰, was collected for the purpose in the Gulf of Guinea.) This procedure obviated any salt-error in the estimation. The sensitivity of the method varies slightly with the intensity of colour, and is at its lowest, $\pm$0·05 mg. atoms $P/m.^3$, at concentrations of 3·00 mg. atoms $P/m.^3$ All the phosphate samples were analysed within a maximum of 10 hr. after collection.

ESTIMATION OF DISSOLVED OXYGEN

Winkler's method was used for the determination of dissolved oxygen. The samples were stored under a water-seal in the precipitated form ($Mn(OH)_3$) and all were analysed within 20 hr. of collection. Standardization of the sodium thiosulphate was effected by titration with an approximately equal strength (0·22 N) solution of potassium iodate. This standard, kept in a slightly alkaline solution, proved very stable even in the most adverse climatic conditions.

For normal sea-waters the Winkler method works very well, but in the presence of certain contaminants the analysis can lead to erroneous results. It was to be expected, therefore, that in the vicinity of the South-west African coast, where organic production is very high, such contamination might be encountered. The principal sources of interference were considered to fall into three groups:

1. Large quantities of micro-organisms in the samples.
2. Relatively high concentrations of nitrites.
3. The presence of hydrogen sulphide.

Organic matter can affect the Winkler estimation in two ways. First, direct oxidation of organic matter is very rapid around pH 12·0, and this might occur during the initial alkaline stage of the analysis. Secondly, the iodine when liberated is liable to be absorbed by the micro-organisms. As it was not possible to analyse all the samples immediately after collection, and as they would have to be stored in one or other of these two stages, it was necessary to decide which course would cause the

least interference. Experiments on the determination of oxygen in dilute dinoflagellate cultures were made at the Marine Biological Association's Laboratory at Plymouth before the cruise. Those demonstrated that the principal interference took place through absorption of iodine by the dinoflagellates. Samples titrated immediately after acidification and liberation of the iodine showed a higher oxygen content than those titrated 2 hr. after acidification. In this period the mean absorption of iodine was equivalent to 0·4 ml. of oxygen per litre at 15° C. in 3 hr. No difference was observed in samples stored in alkaline-precipitated condition for periods up to 10 hr. It was decided, therefore, to store samples in the latter condition.

Allee and Oesting (1934) found that quantities of nitrite of 0·71 mg. atoms N/m.^{3} and over were sufficient to affect the Winkler method. The interference occurs through the nitrite's liberating iodine from the potassium iodide and giving a greater quantity of iodine than would normally be released through the acidification of the manganic hydroxide precipitate in the presence of potassium iodide. The error is, of course, to overestimate the amount of oxygen present. 0·71 mg. atoms N/m.^{3} is quite a high figure for the sea, but as no nitrite estimations were made the extent of any error likely to arise was unknown. The modified Winkler method used to deal with hydrogen sulphide, however, also removes any interference due to nitrite.

Some of the sediments on the sea-bed in the region of Walvis Bay are populated by sulphate-reducing bacteria, whose activity results in the production of hydrogen sulphide. This gas, liberated into the overlying water, appears to coexist, in a dynamic state, with the dissolved oxygen (Durov and Turzhova, 1947). To obtain a true estimation of the oxygen content at a particular time and position it was necessary, therefore, to put an end to the oxidation-reduction reaction as soon as possible after sampling. Although Alsterberg's method (1926) would have been preferable we tried to accomplish this by using the Rideal–Stewart modification of Winkler's method, which could conveniently be carried out with the chemicals available on board. The method consists of a preliminary oxidation, carried out by treating the acidified water sample with potassium permanganate. When the reduction is complete any remaining permanganate is destroyed by the addition of potassium oxalate, after which the normal Winkler method is continued.

Parallel determinations on samples from Walvis Bay with both the Rideal–Stewart and unmodified Winkler methods gave the results shown in Table 1.

Table 1. *Dissolved oxygen content of water-samples from Walvis Bay*

Sample no.	Dissolved O$_2$ content (c.c. O$_2$/l)	
	Unmodified Winkler	Rideal–Stewart Winkler
1	0·00	0·03
2	0·00	0·09
3	0·00	0·11
4	0·05	0·13
5	0·30	0·38
6	0·46	0·51
7	0·64	0·80
8	0·68	0·88

Oxygen determinations on water-samples taken in Walvis Bay using both the Rideal–Stewart and unmodified Winkler methods. The samples have been arranged in order of concentration, and they were all analysed at the same intervals after collection.

A further test was carried out on four similar samples with the unmodified Winkler method. Two of the samples were analysed immediately after collection, while two were kept for 4 hr. before analysis. The first two showed respectively 0·41 and 0·39 cc. O$_2$/l. more than the second two. If this

reduction in the oxygen content of the second two samples was solely due to reduction by hydrogen sulphide, the result would indicate that a concentration of about 0·8 cc. H_2S/l. had been oxidized in the 4 hr. which elapsed. Unfortunately we had no opportunity of making more experiments of this nature, and it is not possible to say precisely how efficiently the Rideal–Stewart method accomplished the task which it was set.

TREATMENT OF THE PLANKTON SAMPLES

The microplankton catches (N 50 V samples) were worked up by a counting technique essentially similar to Hensen's method, as described by Steuer (1911). From the whole sample, thoroughly mixed by agitation in a spherical Stempel flask, subsamples were drawn off with an 0·5 ml. Stempel pipette and placed in a cell on a large slide, ruled with squares of approximately 1·8 mm. These can almost be contained within one field of the low-power objective ($\frac{2}{3}$ in.) of an ordinary compound microscope. The cell was originally intended for counting centrifuged samples at sea, where a cover-glass must be used. It measured approximately 10×24 of the squares and 0·4 mm. in depth so that almost exactly 0·3 ml. of fluid could be contained in it, trapped under a large rectangular cover-glass. For this work cover-glasses were not used during the early stages of the counts, but the cell was found very convenient to contain the larger volume of fluid while spreading it over the face of the slide with a mounted needle. When difficult rich subsamples prolonged the counting, or higher powered objectives than the $\frac{1}{6}$ in. were needed for identification, it was found that evaporation at room temperature allowed one to apply a cover-glass after some 45 min. Most of the counts took more than 2 hr. and continuous observation for a longer period increased personal error due to eye-strain, though a brief pause sufficed to counteract this. Thus the use of a cover-slip during the later stages, to prevent the preparation drying up, became an essential part of the technique.

The rulings on the face of the slide enabled one to resort to higher magnifications, or to recapitulate when necessary, without 'getting lost', and it was thus quite practicable to work through the whole subsample, using a large mechanical stage. A very abundant inshore pennate diatom, *Fragilaria karsteni*, has the habit of growing in very long ribbon-shaped colonies, and it was found that the numbers of frustules could be estimated rapidly, and with a high degree of accuracy, by measuring the ribbons under low power with a micrometer eyepiece, then measuring the width of a few individual frustules under high power and dividing appropriately.

For the method as a whole to be successful the subsample must not be so thick that individual cells or colonies obscure each other unduly. With large samples this was avoided by preliminary fractionization and adjustment of volume, using a large (5-ml.) Stempel pipette and measuring cylinders for added water. Errors were obviously increased by such a crude method, but could be reduced by making separate counts at different dilutions for the more difficult stations, and pooling the results; and by such expedients as counting large or conspicuous species at normal dilutions where the density of smaller dominant species necessitated further subsampling before they could be counted. When the general nature of the flora had become familiar it was nearly always found possible to judge the extent of fractionization and dilution needed from the settlement volume and macroscopic appearance of the sample. At worst two trials enabled the necessary adjustment to be made.

The main object of this line of work was to study the spatial distribution of the larger phytoplankton organisms in relation to the hydrological features of the area. Obviously such estimations can bear little direct relation to the total amount of phytoplankton present—it has long been known that there are many autotrophic organisms among the minute forms that escape the finest nets—but it is claimed that, so far as the diatoms and larger dinoflagellates are concerned, they show up the grosser quantitative differences quite fairly in areas such as this, where the gradient of population density is very

steep. The quantitative differences are so marked, as between the coastal current and the oceanic surface-water to the west, that even such crude measures as settlement volumes can be shown to be statistically significant.

The numerically estimated totals of Protophyta, and of dominant groups or species, when plotted logarithmically, showed distributional patterns in good agreement with hydrological features independently assessed. Moreover a 50% alteration, in either direction, of the values assigned to the contour lines made little difference to their position on the chart. Crude as the method undoubtedly is, errors of this magnitude are very unlikely and the counts are therefore believed quite fairly to represent the broad outlines of the distribution of such organisms as were retained by the finest grade of bolting-silk. All the counting was carried out ashore, while working at the Plymouth Laboratory.

The great variety of the Benguela current plankton is shown by the fact that although only diatoms and *Ceratia* were identified down to species, the raw counts include some 200 categories of organisms. This unfortunately makes it impracticable to publish them in full, but the tables of derived values, dealing with group totals and relative abundance of more important categories, show the number of categories observed during each estimation, in addition to volumes and fractions of samples examined. This should give some idea of the qualitative richness of the microplankton of the area in addition to its great quantity.

For the study of *relative* importance of the various categories these counts should be quite satisfactory since several hundred individuals were involved in most of them. More than 300 individuals were counted at 79% of the stations, and at more than half of these (42% of the total) over 600 individuals. Only at the very poor stations, where concentration (as opposed to dilution) might greatly have increased the manipulative errors, did the numbers fall below 300 per station. These poor samples constituted 21% of the total and the numbers of individuals counted in them ranged from 90 to 288 with an average of 209.

Changes in relative abundance are important when it can be shown that species or groups have 'indicator value'; that their distributions are mainly restricted to water-masses that can be distinguished by their physical attributes. When this can be established, plankton distributions may provide evidence of water-movement and of areas of mixing, of real value to the physical oceanographer and to fishery research.

It has proved impossible to complete group-sorting of the zooplankton collections in time to consider them fully in this report. The vertical net series for the first survey have been almost completely sorted, and individual zoologists able to work up some of the groups have come forward. In this general description of the plankton conditions, we have mentioned only such important (and often elementary) features as became apparent at the sorting stage, adding specific identifications confirmed or established by specialists whenever it has been possible to do so. Some reports on single groups have already appeared and acknowledgements to those who are aiding the work in this way will be found in the zooplankton section. Examination of second survey material has only been completed for pilchard eggs, larvae and post-larvae, the importance of which became apparent at an early stage. A preliminary account of their distribution has already appeared (Hart and Marshall, 1951).

Complete sorting of all groups, except Protozoa, Coelenterata, Copepoda and small nauplii (mainly of Copepoda), has been attempted. For the latter subsampling proved the only practicable procedure, and at a few very rich stations subsampling had to be adopted for some of the other groups also. Nearly all the work has to be carried out under a binocular dissecting microscope, since many of the animals were much smaller than their relatives in cold seas. We are very grateful to Dr M. V. Lebour, and others working at Plymouth who have occasionally corrected or confirmed provisional identifications for us.

ITINERARIES
Survey 1 (march)

On the afternoon of the 1 March 1950, the 'William Scoresby' proceeded southward from Lobito Bay towards the outer end of the first line of stations (WS 964, see Fig. 1). This course involved some two days steaming, and it was not until early on the morning of 3 March that the first indications of the Benguela current were met with. In 16° 13′ S., 11° 31′ E. the distance thermograph revealed a sudden decrease of sea temperature from 27° C. at 02.45 hr. to 20·5° C. at 03.45 hr. At the same time the echo-soundings showed a sudden increase in depth from 110 m. to 439 m. followed by a return to the shallower 110-m. level. During the day the temperature rose again, but not to its initial (tropical) level. Evidently the ship had crossed one of the most northerly patches of the cold upwelled water so characteristic of the Benguela system. This may possibly have been associated with the indentation of the continental shelf indicated by the soundings.

The projected position of the first station was reached just after noon on the 4th, and during the rest of that day six stations were completed, at intervals of some 18 sea-miles, as we worked eastwards in towards the land. The weather was moderately favourable at the first station (WS 964) and improved as land was approached. Station WS 970, marking the inshore end of the 'Möwe Point' line was completed at 01.27 hr. on the 5th, and the course was continued south-westwards working the five stations of the northern intermediate line (WS 971–5) throughout that day. The wind and sea increased as we proceeded offshore, but fortunately moderated again on the morning of the 6th when we reached the first full station position, WS 976 in 22° 50′ S. 11° 38′ E., the outermost station of the 'Walvis Bay Line'. This and the following day were spent in completing stations WS 976–9, and on the morning of the 8th, after stations WS 980 and 981, the ship went into Walvis Bay. Here some arrears of chemical analyses were dealt with and some useful information on local fishery matters was gleaned from some of the residents.

Leaving Walvis Bay on 9 March, the ship passed through large areas of discoloured water, mainly of an olivaceous colour, with small patches of a deeper brown or reddish colour. Surface samples were examined, showing immense numbers of diatoms with but few *Gymnodinium* spp. The more densely coloured patches contained a small dinoflagellate, which subsequent work on preserved material has shown to be *Peridinium triquetrum*. Seals (apparently fur-seals) were seen playing lazily in the discoloured water. Our course lay south-westwards, and the middle line of bathythermograph stations was completed by 04.38 hr. on the 10th. At 08.05 hr. the first full station of the 'Sylvia Hill' line was begun in fine weather, and the clear, almost metallic blue colour of the water here formed a sharp contrast to the turbidity of that inshore. The Nansen–Pettersson water-bottle was visible at a depth of 20 m. By the end of the station, however, the water was obviously more opaque, and steaming eastward we again passed through more discoloured patches within the hour, and continued to do so until 17.05 hr. At station WS 986 there was much macroplankton about the ship; many Ctenophores, mainly in a necrotic condition, and colonies of Salps, were taken out with the hand net. Small shoals of fish were seen, but could not be sampled.

The 'Sylvia Hill' line was completed before dawn on the 11th, and proceeding south-westwards again, on the southernmost line of bathythermograph stations, an otter trawl was used at WS 990. The catch contained several large hake, a fair selection of the other common ground-fish of the region, and some good specimens of Stomatopoda. The outer station of the 'Orange river' line, WS 996, was reached at 15.55 hr. on the 11th and the remaining stations of this line were continued in fine weather, being completed by 03.45 hr. on the morning of 14 March.

Further observations would, of course, have been desirable, but the commitments of the rest of the

programme, and the rather urgent need for repairs to some of the auxiliaries, was such that we had been fortunate in carrying out most of the coverage planned before proceeding to Simon's Town, where we arrived on 16 March.

SURVEY II (SEPTEMBER–OCTOBER)

The second survey of the current had not originally been contemplated, but preliminary examination of the results of the first survey indicated that a repetition would be very desirable, and subsequently a necessary alteration in the programme of the ship made it possible. It was decided that certain extensions to the programme would greatly enhance the value of the repeated stations. Details of this expanded programme were decided upon by Mr Clarke, and its value can readily be appreciated from the results obtained.

Leaving Simon's Town on 19 September 1950, we worked a series of bathythermograph stations (see Fig. 2) round the Cape of Good Hope, and up to the Orange river mouth where the ship arrived on 21 September. Numerous fur seals were encountered on this journey, and several fairly extensive patches of olivaceous coloured water were crossed. Full stations were worked in approximately the same positions as on the first survey, while the ship steamed out along the Orange river line, and this was completed on the 23rd. Our course now lay north-eastwards, repeating bathythermograph observations, and the inner end of the 'Sylvia Hill' line was reached on the 25th. The full stations WS 1064 and 1065 were completed by about midday on the 26th, and then a slight diversion was made to take some bottom samples to the north of the line. This included a circumnavigation of Hollam's Bird Island, a guano island concerning which the following extract is quoted from Dr Clarke's journal:

By 1700 hrs. we had approached to within half a mile of Hollam's Bird Island. As we steamed over the shelf which surrounds the island, the echo-sounder showed several fish shoals, densely packed, in ten fathoms of water.

The island is small and low, not rising more than forty or fifty feet in its highest part....An elaborate sheerlegs is a conspicuous feature of the island, and its skeleton framework overhung the rock strandflat and adjacent breaking water, like some part of the wrecked architecture of an amusement park—even to the strings of electric lamps counterfeited by rows of cormorants sitting equally spaced along the struts of the sheers. Near this structure stood a small roughly built shed—the island is visited at times by the government guano collectors.

The higher ground lay back from the landing place, and from these higher parts the cliffs fell away steeply, the yellowish rock face being boldly streaked with white spillings of guano. And everywhere, crowded thickly upon the slopes, and as far as the highest point, were the fur seals. As we came within half a mile we could hear their barking above the drumming of the surf. From a distance it was a dog-like noise, like many packs of hounds, only deeper in tone. The din must have been tremendous for anyone landing there and walking among the crowded seals. There were many hundreds of seals on this scrap of rock: I made no estimate, but Mr Currie put the population around 1300, probably more. The island with its multitudinous seals looked like a currant cake, of the kind children call 'flies' funeral'. The shiny coats caught the sun, and reflected so many black points, some in slow movement and some quite still, on the wet slopes and crags. Most movement was on the lower rocks, near the landing-place, where the heavy surf was lively with heads and flippers and the strandflat populous with seals coming and going from the water.

Although I could only, from the distance at which we sailed, identify among the birds the cormorants on the sheers, there were obviously great numbers of birds grouped among the seals. At 1700 I counted flocks of about fifty cape gannets, fifteen cape cormorants and five southern black-backed gulls; and also five cape pigeons, although these were farther off.

The visit to Hollam's Bird Island was worthwhile if only to have seen so much life on this tiny island off the barren 'Skeleton Coast'—life so teeming that only a scene in Antarctic seas is comparable. It brought home more vividly than anything else how real and astonishing are the effects of the productivity of the Benguela Current.
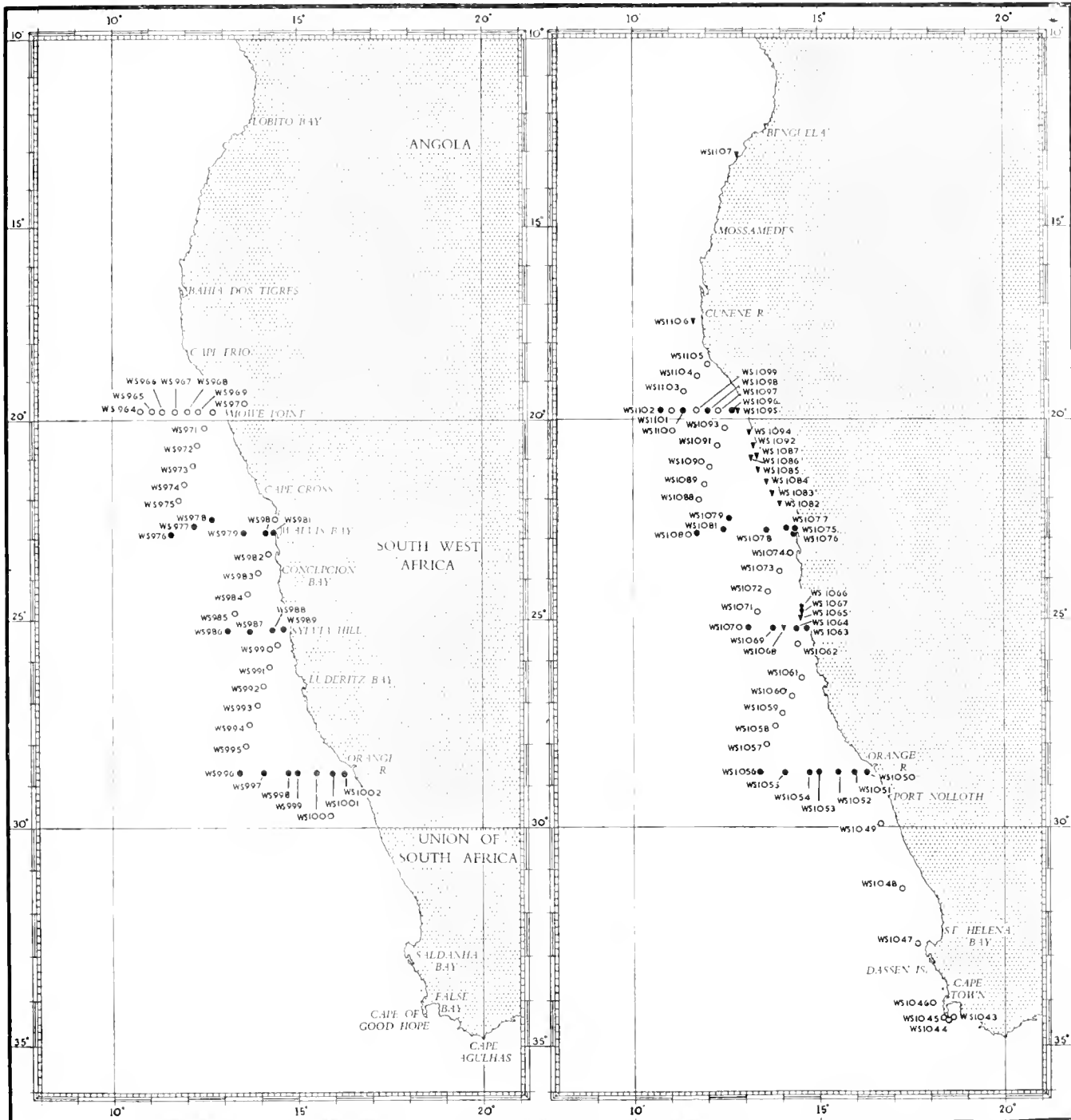
Fig. 1. Station chart, survey I, March 1950. Positions of 'bathythermograph and phytoplankton' stations are shown by open circles, those of 'full' stations by closed circles.

Fig. 2. Station chart, survey II, September–October 1950. Symbols as in Fig. 1. Solid inverted triangles indicate positions of bottom sampling-stations.

After visiting Hollam's Bird Island we completed the full stations of the central line, and the ship steamed towards Walvis Bay making bathythermograph observations at WS 1071–4. On the 29th the 'Walvis Bay' line was started and worked out to WS 1079, after which further station work was delayed by a strong southerly gale which set in. The ship was hove-to for two days while the gale increased to force nine (Beaufort), and not until the afternoon of 2 October did it abate sufficiently to permit us to continue observations, whereupon stations WS 1080 and 1081 were completed, and the ship sailed to Walvis Bay.

After we left Walvis on 6 October, a series of bottom-samples were taken up past Cape Cross (WS 1082–7), and then the bathythermograph observations were resumed, and continued up to Möwe Point, with two detours (WS 1092 and 1094) inshore for bottom sampling, *en route*.

In this area, and also on the 'Möwe Point' line station, numerous large shoals of fish were encountered. Here again, we quote from Dr Clarke's Journal:

9th October, 1950. In the early hours of today (0100 to 0430) the officer of the watch reported that the ship steamed through large shoals of small fish, like herring or pilchards. This was in position 20° 35′ S., 12° 55′ E. to 20° 10′ S. 12° 30′ E.

Again from 2015 to 2145 (around 19° 43′ S., 12° 36′ E.) we found ourselves passing multitudinous shoals of fish. It was a dark night, and I stood and watched the shoals scatter from our approaching forefoot, one after another, betrayed by a burst of greenish blue luminescence, so that the shape of each fish showed up in ghostly outline. Below the forefoot, and fanning out to port and starboard, the shoals were like the showery explosion of roman candles under water.

I counted a hundred shoals (each estimated at > 100 < 1000 fish) appearing in 4 minutes 23 seconds, or 0·4 shoal (> 40 < 400 fish) per second; the ship was then steaming at about eight knots.

The ship was stopped in an attempt to catch some of these fish with both baited hooks and jiggers, so that the species might be determined, but all efforts were unsuccessful.

Further station work was continued with two short interruptions to mark some whales, and the second survey completed on 12 October.

Two bottom-samples were taken to the north, at WS 1106 and 1107, to ascertain if the 'azoic' mud extended so far north. Approaching station WS 1107, between 14.15 and 15.21 hr. on 14 October, patches of blood-red water were observed, some 20–30 yards across, a bucketful was collected, and microscopic examination of preserved subsamples showed that the organisms causing the discoloration were almost certainly ciliate protozoa such as have previously been seen to cause red water elsewhere (see p. 255).

COASTAL GEOGRAPHY AND BOTTOM TOPOGRAPHY

The west coast of South Africa stretches in a more or less N.N.W. direction from the Cape to about 18° S., then continues north and N.N.E. into the Bay of Benguela. Practically the whole length of this coast is characterized by a narrow coastal belt of low-lying land gradually ascending to the high interior plateaux at a distance of about 80–100 miles inland. The coastal belt is fertile in the south, but gradually passes into scrub, and north of 30° S. is a truly arid desert. This desert, which continues to about 14° S., is known in South-west Africa as the Namib. It is almost completely waterless, although heavy dews occur, and the small annual rainfall (Fig. 3) generally occurs in a very short space of time, draining into the Atlantic almost as quickly. The dew is sufficient to support a very scanty xerophytic flora, but cultivation is only possible up country in the more fertile valleys. The presence of the desert is principally due to the cold water lying along the coast, which causes condensation from the lower layers of the air above it (Scherhag, 1937), and acts like a mountain range, leaving the land to leeward in its rain shadow. North of the desert, in Angola, the sand gradually gives way to wooded country within the range of the seasonal tropical rains.

Although in itself arid, the South-west African coast has a very large drainage area, extending across the interior to the western slopes of the Drakensberg mountains on the other side of the continent. Practically all of this drainage, however, is collected in the Orange river, and other rivers along the coast are only periodic torrents, during the summer rains in the south-west.

The topography of the sea-bed is shown in Fig. 4. It appears to be affected in a large degree by the

Orange river, for the great underwater promontory sweeping seawards from the river mouth suggests a considerable alluvial deposition from the great drainage system.

Although more data are still needed, the representation of such major features of the sea-bed seems adequate for our present purpose. The chart (Fig. 4) has been constructed from:

1. The most recent Admiralty Charts of the region.
2. Carte Bathymetrique Internationale. A IV (International Hydrographic Bureau, Monaco, 1938).
3. 'Meteor' expedition bathymetric charts (Stocks, 1941).
4. Soundings made by the 'William Scoresby'.
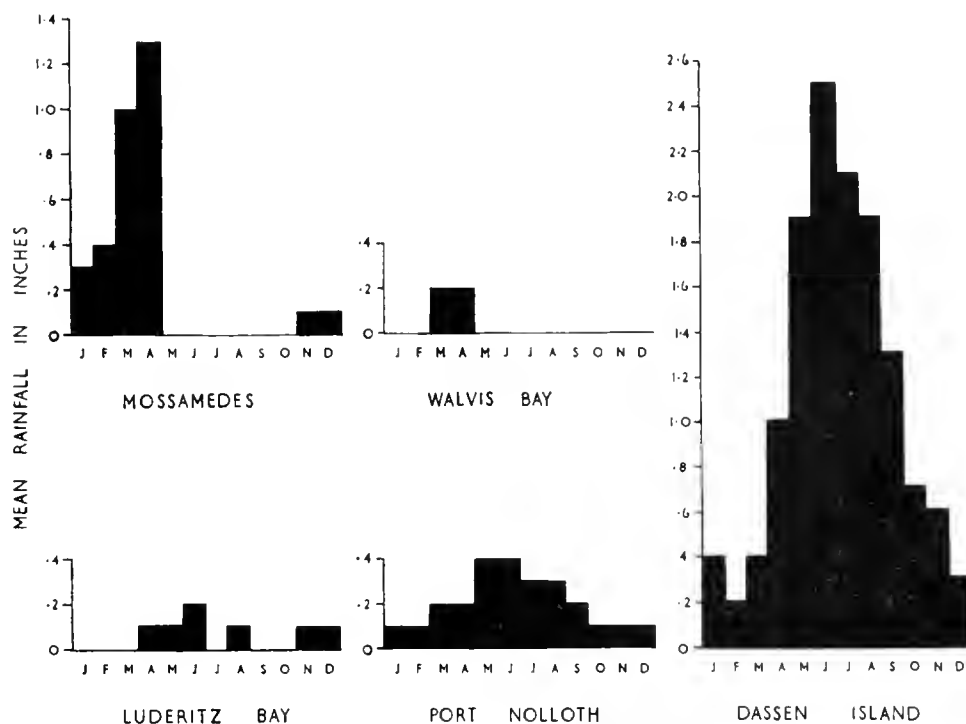
Fig. 3. Mean annual rainfall in inches, at five points on the South-west African coast: Mossamedes (15° 12′ S.), Walvis Bay (22° 56′ S.), Luderitz Bay (26° 39′ S.), Port Nolloth (29° 14′ S.), and Dassen Island (33° 26′ S.). (From data in Royal Naval Meteorological Service and South African Air Force, 1944.)

Over the greater part of the area covered by our surveys, the continental shelf, defined approximately by the 200 m. contour, is about 40 miles broad, widening to about 90 miles off the Orange river mouth, and to 70 miles off Walvis Bay. Off Concepcion Bay, in 24° S., there is a sharp indentation on the shelf edge, and as at Luderitz Bay the shelf is less than 20 miles broad.

North of 20° S. the shelf narrows, and between 16° and 13° S. is almost non-existent, the slope falling straightway from the coast into the depths of the Angola Basin. The shelf edge off Bahia dos Tigres is much dissected into deep valleys which extend to depths of 1000 m.

The bottom slopes away fairly steeply from the coast to the 100-m. contour along most of the coastline, and then more gradually to the shelf-edge, forming virtually a submarine plain, a feature most pronounced off the Orange river. From the shelf-edge there is a fairly gradual and constant slope to 3000 m., interrupted only off the Cape Peninsula where deep canyons are numerous between 500 and 3000 m., and in 20° S. where the continental slope is very gradual and at 1000 m. grows into a buttress forming the northern end of the Walvis Ridge.

The Walvis Ridge leaves this buttress in a westerly direction at 3000 m., and runs southwards and then to the west again to link up with the central Atlantic Ridge. In 25° S., 6° E. there is a prominent
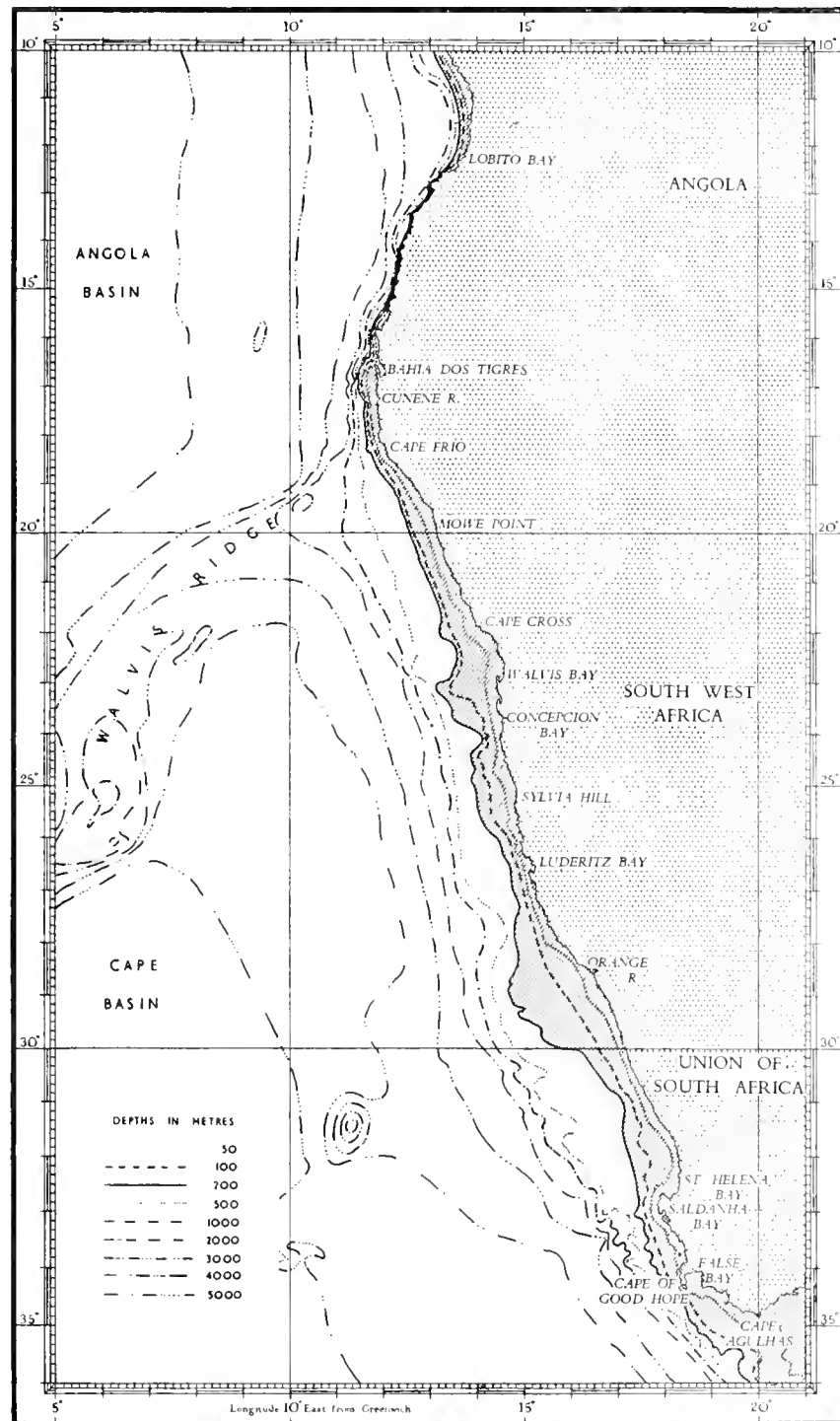
Fig. 4. Topography of the sea-floor of the South-west African region. Depths in metres. The hatched area shows the extent of the continental shelf. For origin of data see text.

peak on the ridge rising to less than 1000 m. from the surface. Soundings over this deeper part of the ridge are scarce and there may be a gap in about 22° S., but even so it can be little more than a break in the 3000-m. contour, and the results of the 'Meteor' expedition have already demonstrated the significance of this ridge in the circulation of the deeper waters. The Walvis Ridge forms a very effective barrier to northward movement of the Antarctic bottom water, the potential temperature of the bottom water in the Cape Basin being less than 1·0° C., while in the Angola Basin it averages more than 2·0° C. (Wust, 1935).

In 31° 20' S., 11° 20' E., there is what appears to be a sea-mount rising from 4000 m. to within 1000 m. of the surface, but this is evidently an isolated feature.

Soundings taken on the 'William Scoresby's' line of stations are plotted in the respective vertical sections (Figs. 12–18, 22, 23, 25–30). In these diagrams the vertical scale is, of course, very exaggerated (about 320 times). The absence of much shelf, with development of a fairly gradual slope, is clear on the most northerly section, while on the Walvis line there are two shelves about 25 miles broad, the upper just over 100 m. deep, and the lower at 300 m. At Sylvia Hill the coast slopes away steeply to a narrow shelf at 200 m., while on the Orange river line the shelf is much broader, about 50 miles, at 175 m. This latter represents the northerly part of the promontory referred to off the Orange river.

METEOROLOGY
WIND SYSTEMS

The movements of the sea are so closely linked with those of the overlying atmosphere that any account of the oceanographical phenomena of a region must necessarily take into consideration the prevailing meteorological conditions. Fortunately, off South-west Africa these seem to fluctuate so regularly (apart from minor variations) that a normal or 'average' pattern can be formulated, which serves as a background against which the data relating to the periods of these two surveys can be considered. The general account which follows is based upon data collected by the Meteorological Services of the Royal Navy and the South African Air Force (1944), supplemented by the work of Dr S. P. Jackson (1951) who has long been interested in the weather of South-west Africa.

The wind system over the South-west African waters depends mainly upon the subtropical high-pressure region which overlies the South Atlantic. The latitudinal axis of this anticyclonic centre is situated between 26° and 30° S. From the centre the pressure gradient decreases gradually to the north, but to the south, where it borders on the zone of the 'westerlies', the gradient is much steeper. Round this high-pressure region the winds blow anti-cyclonically, so that off South-west Africa, which lies in the eastern side of the pressure system, the winds are predominantly south or south easterly. The coastal region, however, lies in the transition belt between the oceanic and continental pressure systems, and so in the proximity of the coast the winds become modified by the fluctuations between the two systems. It is necessary, therefore, to distinguish two separate wind regions—that offshore where the South Atlantic anti-cyclone acts alone, and the other inshore, where both the oceanic and continental pressure systems play a part.

The trade wind

In the summer, when the anti-cyclone lies in about 30° S., strong constant winds are produced, which affect the whole oceanic region northwards from the Cape. About 80–85% of these winds are south-easterly, and they blow with an average velocity of 11–21 knots. At the Cape peninsula these 'south-easters' are a prominent feature of the summer climate, but the strongest winds are farther north, between 25° and 30° S. North of 25° S. both the velocity and constancy of the trade winds diminish.

In winter time the anticyclone moves northwards and intensifies slightly—generally about 2 millibars higher than in summer—so that the centre of highest pressure comes to lie in approximately the latitude of Luderitz Bay (26° S.). Owing to the steep southward pressure gradient the trade winds in 30° S. then become intermittent. This northward displacement of the pressure system brings the Cape region under the influence of the depressions of the westerlies, which, travelling eastwards from the south-west Atlantic, bring rain to South Africa, accompanied by the attendant cyclonic variation of the winds. The effect of these depressions extends as far north as Port Nolloth, where they produce
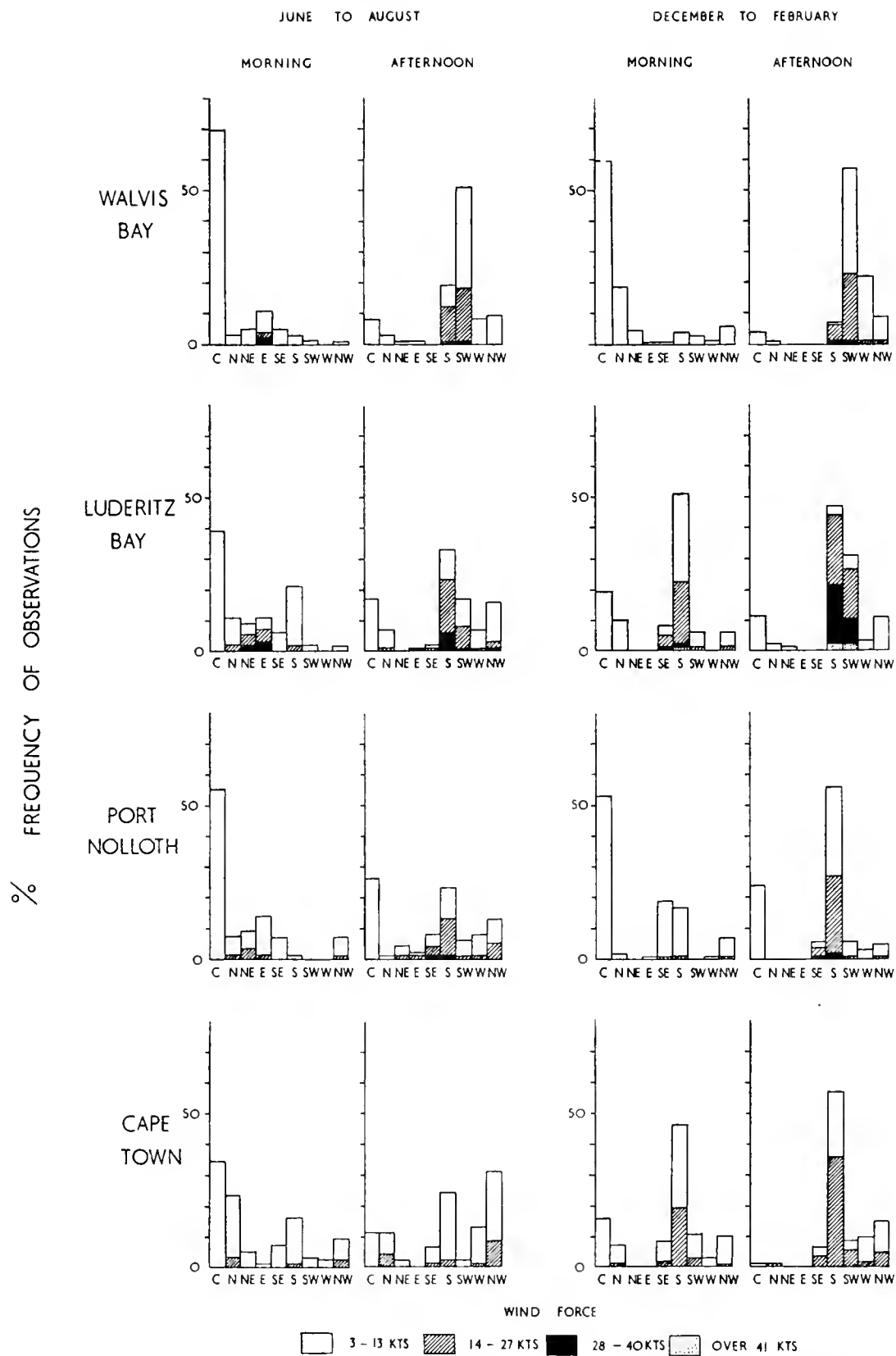
Fig. 5. Percentage frequency of coastal winds in winter and summer. (From data in Royal Naval Meteorological Service, etc., 1944.)

a light, but quite pronounced winter rainfall (Fig. 3) which does not occur in the more northerly parts of South-west Africa. The region of strongest winds also shifts north in winter, and lies in about the latitude of Walvis Bay, where 30% of the trade winds have a velocity of over 16 knots.

The coastal winds (Fig. 5)

Although the inshore region remains under the influence of the South Atlantic anti-cyclone, the winds are also affected by the variations in pressure over the continent, and as this fluctuates diurnally with the heating and cooling of the land, so the coastal winds develop a marked diurnal variation (Fig. 5). During the day, when the land is warmed up, the overlying air mass becomes light, and this causes the cooler, more dense air over the sea to flow inland. This continues until equilibrium is regained, and stable conditions are once more set up. On the whole these coastal winds, while they last, are stronger than those at sea, but when the trade is blowing strongly over the open ocean one generally finds the coastal winds are also stronger.

In summer (December–February), when the anti-cyclone is in its southern position, south winds are prevalent on the coast as far north as Luderitz Bay (Fig. 5), generally having an easterly component in the morning. This seems to be the effect of the anti-cyclone exerting its influence on the relatively stable air mass over the coastal waters and land during the night and early morning. As the land warms during the day, however, the wind veers round to the south and south-west and intensifies, reaching at Luderitz an average velocity of 22–27 knots. This may occur fairly early in the day, and the sea-breeze then continues until after nightfall when the pressure systems become balanced, and the anti-cyclone once again becomes the dominating influence. It will be remembered, however, that in summer the anti-cyclone has its greatest effect in the Luderitz Bay region, and that north of this its influence steadily decreases, so that at Walvis Bay the stable air mass during the dark hours appears to be little affected by the anti-cyclone, and the conditions experienced there during the night are either complete calms or light northerly winds. As the day progresses, and the temperature effect comes into play, the wind *backs* to the west and then S.S.W. from which the sea-breeze develops just after noon, and blows with a mean force of 11–16 knots.

In winter, as might be expected with the northward shift of the pressure systems, the seasonal variation is much more pronounced south of Orange river than on the more northerly part of the coast. With the westerly depressions, the Cape receives winds more or less evenly distributed between north and south from the westerly sector. A marked feature of the winters is the north-westerly gales, which along with south-westerly weather are associated with the passage of the depressions. These features are less prominent at Port Nolloth where the trade and the diurnal variations begin to take effect.

Occasionally, when the anti-cyclone is not strongly developed near the coast, small depressions form close to the shore, and move northwards. On these occasions the sky remains cloudy, and a light north-west wind sets in with a force of about 7–10 knots. These conditions have a remarkable effect upon the sea temperature, which increases suddenly and has been known to reach as much as 23·9° C. at Walvis Bay.

At both Luderitz Bay and Walvis Bay there is a marked increase in easterly winds during the mornings in winter time (Fig. 5), but in both cases they are replaced with the much stronger south-westerly breeze in the afternoons. Pressure is high on the continental plateau in winter and, coupled with the lower pressure over the coast, leads to an outward push of air from the plateau. This usually becomes obliterated later in the day, partly by a diurnal variation of the east wind itself further inland. Amidst these easterly winds, when conditions are favourable, the noteworthy 'Berg winds' occur, which, blowing with considerable force towards the coast, make conditions extremely unpleasant on account of their high temperature compared with the generally cool coastal climate.

The Berg winds are extremely hot, dry winds which blow seawards across the desert, carrying much sand and dust. They may last from a few hours to several days. A temperature of 115° F. was recorded at Port Nolloth one day during a Berg wind. The highest recorded at Walvis is 104° F. but the average lies about 90° F. These winds are most frequent in winter, but can occur whenever the pressure gradient and heating of the surface air inland is suitable. When the 'Willlam Scoresby' visited Walvis Bay on 5 October 1950, a typical Berg wind was encountered. It blew for 4 or 5 hr. at 17–21 knots and produced a fine deposit of sand all over the ship. The air temperature reached 99° F. and the wind was uncomfortably dry. The Berg wind does not have much effect over the sea, for coming up against the cool dense air over the water the light hot air diverges upward, away from the sea surface.

In the coastal region, then, the principal wind of force is the sea-breeze, or 'soo-oop-wa' (as the natives call it), S.S.W. in the north and more southerly in the south. Jackson (personal communication) reckons that the sea-breeze probably has a fetch of some 80–100 miles over the sea, that is from its divergence from the south-east trade.

WEATHER PRECEDING AND DURING THE SURVEYS

There are not very many settlements along the desert coast of South-west Africa, and consequently the number of stations which make regular climatological observations is very small. Fortunately, however, records are maintained at Walvis Bay, Luderitz Bay, and Alexander Bay and these are used by the South African Weather Bureau in the construction of synoptic charts of the South Atlantic and South African region. Although we have not had access to the original data we have seen the synoptic charts published at Pretoria and have extracted the data for these three coastal stations as accurately as possible.

While shore observations are useful up to a point, observations at sea would have been much more desirable, but the sparsity of observing ships in the region during the survey makes it impossible to construct a complete enough picture. Most of the observations at sea are made on the main shipping route from Capetown to Sierra Leone, well outside the area of our survey. Such observations as there are, however, have been listed in Table 2, and do serve to show the constancy of the offshore winds, nearly all the observations, at least during survey II, lying in the south to east quadrant.

The only estimate, therefore, of the weather conditions preceding the surveys must be based on the observations made at the three coastal stations; and although the importance of the diurnal variations of the inshore winds has already been explained, all the synoptic charts are based on observations made once daily, at 08.00 s.a.s.t. These shortcomings of the records at our disposal have to be accepted, but must be borne in mind in interpreting the data.

The observations from the three shore stations for the periods preceding and during the surveys are given in Table 3. It can be seen that before survey I the weather at Walvis Bay had been calm or northerly, while at Luderitz Bay, right up to the time the ship visited the locality, the winds had mainly been southerly. At Orange river there had been very little wind for the whole month preceding and during the Survey.

Prior to Survey II, however, conditions were very different. Both Walvis Bay and Luderitz Bay had experienced much stronger winds, mainly from between south and west. As on the first survey, Orange river experienced comparatively calm weather.

So much for conditions on the coast. The constancy of the trade wind has already been shown from the observations at sea (Table 2). From the synoptic charts we can get some further information upon the state of these winds. It has not been considered advisable to calculate the vectors and velocities of the oceanic winds from the isobars, as they are based on so few recording stations. Regular observations come from the South African coastal stations, Tristan da Cunha and St Helena, and the observa-

tions of any ships in the neighbourhood are also included. But considering the vastness of the area affected, these few points must only allow a very approximate picture to be drawn.

The anti-cyclone rarely appears as a single entity, but is usually composed of several distinct high pressure centres slowly travelling across the Atlantic in an easterly direction towards South Africa. When one of these has passed, conditions become more diffuse until the next high pressure centre takes control. The cycle appears to average about four days, but it should be noted that the wind is dependent on the pressure gradient between the anti-cyclone and the lower pressure regions to north and east, and consequently does not vary directly with the position of the anti-cyclone.

Table 2. *Ships' observations (positions approx.) of the wind at sea during the 'William Scoresby' surveys**

Date 1950	Latitude	Longitude	Wind (vel. in knots)
5 March	24° 20' S.	8° 20' E.	S.S.E. 18
8 Sept.	29° 40' S.	11° E.	S.E. 12
13 Sept.	15° 00' S.	8° E.	S.E. 18
13 Sept.	19° 20' S.	5° E.	S.E. 24
13 Sept.	25° 40' S.	9° E.	E.S.E. 24
14 Sept.	26° 30' S.	7° 40' E.	S.S.E. 18
15 Sept.	20° 20' S.	10° 30' E.	S.E. 12
15 Sept.	22° 20' S.	8° 40' E.	S.S.E. 18
16 Sept.	27° 00' S.	12° 10' E.	S.S.W. 6
17 Sept.	27° 00' S.	14° 00' E.	S.E. 12
17 Sept.	22° 20' S.	8° 10' E.	E.S.E. 24
17 Sept.	29° 30' S.	11° 00' E.	S. by W. 6
17 Sept.	25° 30' S.	5° 00' E.	S.E. 18
19 Sept.	25° 50' S.	10° 30' E.	S. by E. 24
20 Sept.	27° 40' S.	12° 00' E.	S.S.E. 18
20 Sept.	22° 00' S.	9° 00' E.	S.S.E. 24
24 Sept.	21° 40' S.	8° 20' E.	S.E. 6
25 Sept.	19° 40' S.	6° 00' E.	S.S.E. 12
25 Sept.	27° 40' S.	9° 00' E.	N.W. 6
26 Sept.	29° 20' S.	12° 40' E.	W. 12
27 Sept.	20° 00' S.	10° 40' E.	S.S.E. 12
28 Sept.	29° 20' S.	13° 40' E.	W. 18
28 Sept.	15° 40' S.	8° 30' E.	S.E. 12
28 Sept.	23° 10' S.	7° 00' E.	S. 12
30 Sept.	29° 30' S.	14° 20' E.	S.S.W. 18
30 Sept.	26° 00' S.	11° 30' E.	S.S.E. 12
30 Sept.	16° 50' S.	5° 10' E.	E.S.E. 30
1 Oct.	21° 10' S.	7° 30' E.	S.E. 30
8 Oct.	18° 30' S.	11° 20' E.	N.N.W. 6
8 Oct.	19° 20' S.	5° 30' E.	S.S.W. 6
10 Oct.	15° 20' S.	7° 10' E.	Calm

* Compiled from information collected by voluntary observing ships for the Meteorological Office.

In February and March 1950, the pressure gradient was not so pronounced as in September–October, and the centres of high pressure lay rather farther south in February and March, in about 30° S. Moreover the anti-cyclone in the September–October period was more intense, and frequently associated with quite marked low-pressure areas over the coastal region. The trade winds were, therefore, stronger and more constant before and during survey II.

Regular observations of wind were of course maintained aboard the 'William Scoresby' throughout both surveys, and these have been rather useful in illustrating some of the short-term effects on the water movement.

During survey I, after the ship left Lobito, the wind was fairly light from the south-westerly sector,

but steadily increased in force and backed to S.S.E. as the outer end of the Möwe Point line was reached. The wind here was blowing with a force of 4–5 Beaufort, but became lighter and veered to the south as land was approached. As we proceeded offshore to the seaward end of the Walvis Bay line it once more became S.S.E. but rather more variable in force, and when Walvis Bay was reached

Table 3. *Coastal winds*

Day	Walvis Bay	Luderitz Bay	Alexander Bay	Walvis Bay	Luderitz Bay	Alexander Bay
	February			*September*		
1	Calm	S.S.W. 30	—	S.W. 6	N.W. 6	S. 6
2	Calm	S. 30	Calm	S.W. 6	Calm	—
3	Calm	S. 30	—	S.S.W. 12	—	—
4	N. 6	S. 12	Calm	S.W. 18	—	W. 6
5	Calm	Calm	—	S.S.W. 18	—	S. 6
6	N.W. 6	S. 18	—	S.W. 18	S.W. 18	Calm
7	Calm	N. 6	S.E. 12	S.W. 18	S.W. 24	Calm
8	Calm	N. 6	Calm	S.W. 6	S.W. 18	S. 6
9	S.S.W. 6	S.S.W. 12	—	W.N.W. 6	Calm	—
10	N. 6	S.W. 18	S.S.E. 6	S.S.W. 6	N.W. 12	—
11	Calm	S. 18	—	S.W. 12	Calm	Calm
12	Calm	S. 12	S.E. 6	S.S.W. 12	S.S.W. 12	Calm
13	Calm	S.S.E. 12	Calm	W.S.W. 12	S. 36	S.E. 6
14	Calm	S. 6	Calm	N.N.W. 12	S.S.W. 24	S. 6
15	N. 6	S. 18	Calm	Calm	N. 6	N. 12
16	Calm	S. 6	Calm	S.W. 18	Calm	—
17	Calm	Calm	—	—	—	—
18	Calm	Calm	Calm	Calm	Calm	S. 6
19	Calm	S.S.W. 18	—	S. 12	—	S. 6
20	—	—	S. 6	W.S.W. 30	S.W. 30	—
21	N. 6	S.E. 6	Calm	S.W. 6	S.W. 30	—
22	N.W. 6	—	Calm	W. 6	S.W. 24	S. 6
23	W.N.W. 6	—	Calm	S.W. 6	W. 6	—
24	Calm	—	Calm	N.N.W. 6	S. 6	—
25	Calm	—	Calm	W.S.W. 6	W.S.W. 6	S. 6
26	Calm	—	—	S.S.W. 24	S.W. 18	Calm
27	S.S.W. 6	Calm	Calm	S. 18	S.S.W. 30	Calm
28	Calm	S. 6	Calm	S.S.W. 12	W.S.W. 18	Calm
29	—	—	—	S.W. 6	N.N.E. 6	Calm
30	—	—	—	S.W. 30	S.S.W. 24	—
	March			*October*		
1	S.W. 6	S.S.W. 12	Calm	S.S.W. 12	S.S.W. 30	—
2	N. 6	S.S.W. 30	S.S.E. 6	W.S.W. 6	S.W. 12	Calm
3	N.W. 6	—	S.S.E. 6	Calm	Calm	Calm
4	Calm	S. 6	—	S.S.E. 12	S.W. 6	Calm
5	S.W. 6	S. 6	—	E.N.E. 6	S.W. 12	Calm
6	Calm	S. 18	Calm	W.S.W. 6	Calm	Calm
7	Calm	S. 6	Calm	W.S.W. 6	Calm	—
8	Calm	S.W. 12	Calm	—	S.W. 30	—
9	N.W. 6	—	Calm	S.S.W. 6	N. 6	S. 6
10	Calm	Calm	Calm	—	—	W. 6
11	· ·	· ·	·	S.W. 12	Calm	Calm
12	—	—	· ·	S.W. 18	Calm	Calm
13	Calm	S.S.W. 6	· ·	S.S.W. 6	S.W. 12	Calm
14	Calm	· · ·	Calm	S.S.W. 12	S.W. 24	—

Wind direction and velocity in knots, extracted for the three stations Walvis Bay, Luderitz Bay and Alexander Bay, from the synoptic charts of the Daily Weather Bulletin, 08.00 s.a.s.t. issued for the above months of 1950 by the Weather Bureau, Pretoria.

it died away completely. These calm conditions persisted until the inner end of the Luderitz line, but towards the Orange river line the wind built up again. It did not, however, become very strong—force 3–4 from the east of south. Off the Orange river mouth the wind dropped.

On Survey II the wind was light after we left Simon's Town, but increased after Saldanha Bay to force 4–5 and remained so until the seaward end of the Orange river line, except for a short calm spell off the Orange river mouth. The passage north to Hollam's Bird Island was very calm, but as we steamed seawards the wind increased from west of south, remaining between S.S.W. and S.S.E., force 4–5, up to Walvis Bay. The course seawards from Walvis Bay was attended by an increasing southerly wind which reached gale force at the outer end of the line, and the ship was hove to against this for nearly two days. The wind then fell quickly and the ship returned to Walvis Bay in light northerly airs. At Walvis Bay the Berg wind already mentioned was encountered, and conditions remained variable with a fair proportion of north-westerly wind up to Cape Frio, north of which the passage became increasingly calm.

SURFACE-CURRENTS

PREVIOUS DATA

Since the ship was working to a strict time-schedule it was impracticable to make any direct observations on the amount of set and drift to which she was subjected. A few occasions, however, presented themselves when trustworthy fixes (stellar or shore) could be correlated with an uninterrupted passage of the ship, thereby giving an estimate of the amount of drift due to wind and currents. With accurate wind observations it was then possible to get a fairly good idea of how much of the drift was caused by the currents alone. These data, although useful in relation to the other oceanographical observations, are insufficient to give any comprehensive picture of the circulation, and for this it has been necessary to draw on other sources of information.

In the South Atlantic Ocean the surface-currents take the form of a large anti-cyclonic gyral of water movement, a circulation impelled principally by the south-east trade winds. These drive the surface water in a westerly direction away from the African coast, and reaching South America it is returned southwards in the Brazil current, and eventually back to Africa in a current flowing more or less in the same direction as the Southern Ocean current but separated from the latter by the subtropical convergence.

Off the South-west African coast there is, therefore, a wind-driven transport of water, principally to the west but rather more northerly in the south of the region (Table 4). It has already been noted that the south-east trade, although very constant in force and direction offshore, becomes much more variable nearer the coast in the proximity of the continental shelf, and consequently, considering purely a wind-driven circulation, one would expect the currents also to behave with much greater irregularity in this region. Unfortunately very few current observations have been made in the coastal region since it lies off the track of the main shipping lanes, but sufficient exist to confirm the irregular

Table 4. *Mean set and drift of the south-east trade wind drift*

	Latitude 12°–18° S.		Latitude 18°–24° S.		Latitude 24°–30° S.	
	Mean set and drift	No. of obs.	Mean set and drift	No. of obs.	Mean set and drift	No. of obs.
Nov.–Jan.	244° 2 miles	141	273° 4 miles	146	316° 5 miles	175
Feb.–April	248° 3 miles	153	280° 4 miles	157	304° 4 miles	165
May–July	285° 3 miles	164	312° 3 miles	170	333° 3 miles	180
Aug.–Oct.	280° 4 miles	160	297° 4 miles	181	314° 4 miles	189

After Hydrographic Department, 1939.

nature of the sets (Mühry, 1864; Koch, 1888; Hessner, 1892; Walther, 1893; Reincke, 1896; Bachem, 1896; Gilchrist, 1903; E.K., S.M.S. 'Sperber', 1907; Pohlenz, 1908; Müffling, 1911; Clowes, 1954), and the British Admiralty Pilot (Hydrographic Dept., 1939), p. 48, remarks with regard to the coastal waters: 'The general set of the current southward of the Congo river is parallel with the coast in a northerly direction at the rate of from 10 to 25 miles a day; but it is very irregular, both in direction
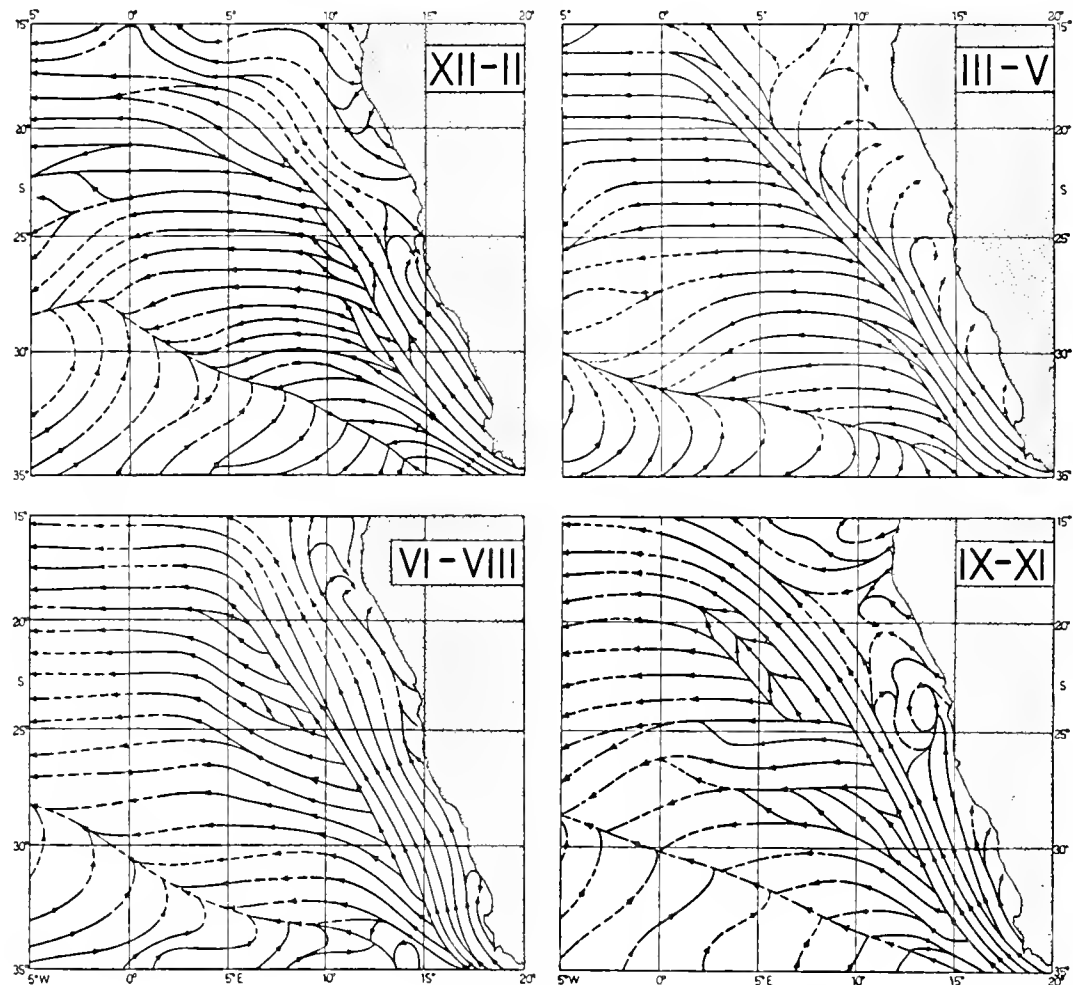
Fig. 6. Charts of surface currents for the four quarters of the year. After Defant, 1936.

and velocity, for sometimes, between October and June, but principally in March, April, and May, the direction of the current is completely reversed, and is found setting southward, and sometimes south-eastward.'

Defant (1936) has analysed the Dutch current observations, and meaned them for four quarters into one degree areas (1° longitude by 1° latitude), and concludes from his analysis (Fig. 6):

Ein Blick auf diese Stromfelder lehrt, dass das Charakteristische in ihnen die in allen Monaten wieder mit nicht zu überbietender Deutlichkeit auftretende *einseitige Divergenzlinie* ist; sie läuft nordnordwestwärts längs der Küste Südwestafrikas von etwa 30° bis über 20° südl. Br.; im Süden ist ihr Abstand von der Küste rund 160 sm, im Norden 300–350 sm. Das Gebiet ostwärts dieser Divergenzlinie, das ist gleichzeitig das Gebiet des Kontinental-abfalles und des Schelfes, hat eine Strömung nordnordwestwärts, also *parallel* der Diskontinuitätslinie und mehr oder minder auch parallel dem allgemeinen Küstenverlauf. Das Gebiet westwärts der Divergenzlinie hat im wesentlichen einen Strom nach Westen.

This interpretation of Defant's appears to correspond fairly well with the data in the possession of the Meteorological Office, the position of Defant's N.N.W. current being similar to that pictured by

the Meteorological Office current charts and more or less on the main shipping lane from Capetown to Sierra Leone.

The current-system of the region affected by the south-east trade wind seems clearly explicable on these lines, but although such an average picture may suffice for navigational purposes even in the more variable inshore region, it cannot assist in the interpretation of the hydrological conditions observed there. The irregularities already referred to show how much the inshore currents must depend upon local wind and local conditions generally. For a significant interpretation of the water movements here a synoptic rather than an 'average' picture would be needed. Existing data do not suffice for this, but a practicable working compromise has been attempted by correlation of the 'William Scoresby's' meteorological observations with the oceanographic data, and with the meteorological records of such other ships as were in the vicinity at the same time.

Currents during the surveys

In March 1950, on the passage southwards from Lobito Bay, the first appreciable effect of current was felt south of Bahia dos Tigres, where a moderate set to the north-east was noted. On the most northerly line of stations (WS 964–70) an allowance of 1° was made on the shoreward course for northerly set, and this maintained a latitudinal line of stations, but it is impossible to say just how much of this was the effect of current as distinct from the wind. At the stations on the outer end of the Walvis Bay line, however, a northerly set of about 1 knot was encountered with a light wind; the observed position of station WS 978 lying 16 miles north-north-east of its intended position. This northerly set was found at the offshore end of the three lines of full stations, and on the Walvis Bay and Sylvia Hill lines gradually became more easterly as land was approached, until at the inshore end of these lines the set was E.N.E. with negligible wind effect.

At the inshore end of the most southerly line, just off the mouth of the Orange river, the set appeared to be S.S.W., against a light wind from the same quadrant.

On the second survey, in spite of the stronger winds, little genuine current effect was recorded. Inshore at Orange river mouth, the ship, while lying-to for the night, showed negligible movement in completely calm conditions. Seawards, however, between WS 1052 and 1053 there was a northwards drift of 14 miles in 14 hr., but this may have been due to the wind. Between WS 1057 and 1061, the first pure current-effect was noted, the ship being set 065° at $\frac{1}{2}$ knot with no wind, and at WS 1063 a slight north to north-east drift was probably due to the light south-west wind, and current must have been almost absent. These conditions continued between WS 1064 and 1067 and on the circumnavigation of Hollam's Bird Island there was no current at all. From 24° 02′ S., 13° 51′ E. to 22° 46′ S., 14° 20′ E. the current set 035° 10 miles in $12\frac{1}{2}$ hr., and later a similar set was observed off Swakopmund where the vessel was stopped and drifted 035° for 3–5 miles in 5 hr. (0·7 knot). Again when stopped off Pelican Point lighthouse at WS 1076 the set was 035° 0·7 knot with no wind. The tide was on the flood then at Walvis Bay, and this may have accounted for the set.

From WS 1081 to Walvis Bay no drift was experienced, and a perfect course was made. As the winds were very light it is probable that there was negligible water-movement. After departing from Walvis Bay no drift of any consequence was encountered, and currents were disregarded in setting courses.

Summing up, the set on both surveys appears to have been very little, but when it was observed it was generally in a northerly direction in the offshore region, becoming more easterly nearer the land. The S.S.W. set off the Orange river is inexplicable at the moment, and it is impossible to say how much tidal streams were responsible for the E.N.E. sets experienced inshore.

OBSERVED DISTRIBUTION OF TEMPERATURE AND SALINITY

This section will be devoted to a description of the horizontal and vertical distribution of the physical and chemical properties of the waters which were surveyed. In the following sections an attempt will be made to relate these observed distributions to the prevailing meteorological conditions and the geography of the area with a view to elucidating the mechanism underlying the process of the up-welling and its fluctuations as we found them.

(a) (b)
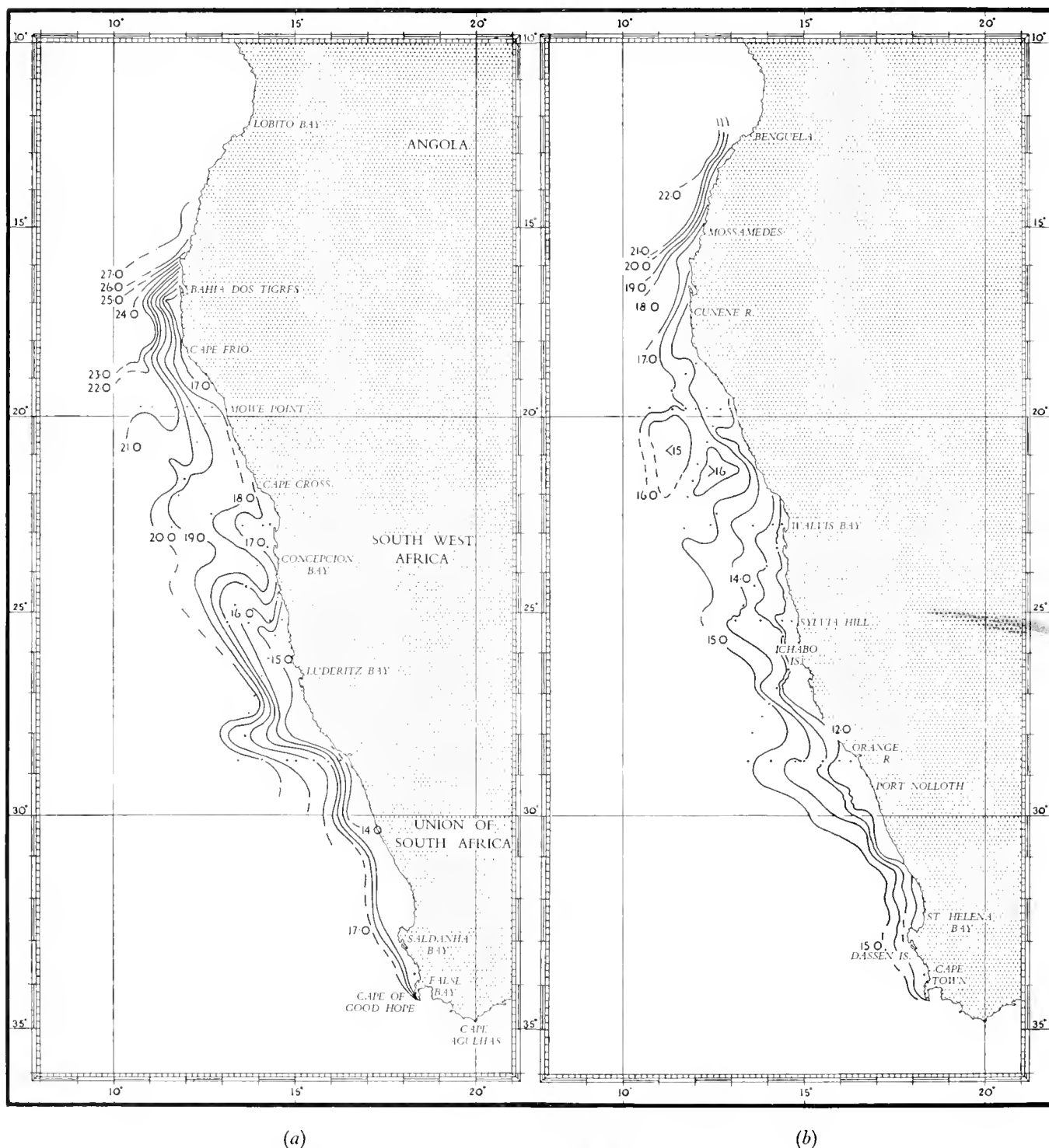
Fig. 7 (a). Distribution of sea surface-temperature (° C.), survey I, March 1950. (b) Distribution of sea surface-temperature (° C.), survey II, September–October 1950. Both compiled from station observations and distant-reading thermograph records.

As the water masses under consideration exhibit a general northward trend, it will be more convenient to treat the results of both surveys from south to north, and not, therefore, in the chronological order of the stations worked during survey I.

The charts showing the distribution of surface-temperature (Fig. 7) and surface-salinity (Fig. 8) show that on both surveys the isotherms and isohalines ran more or less parallel to the coast. Within
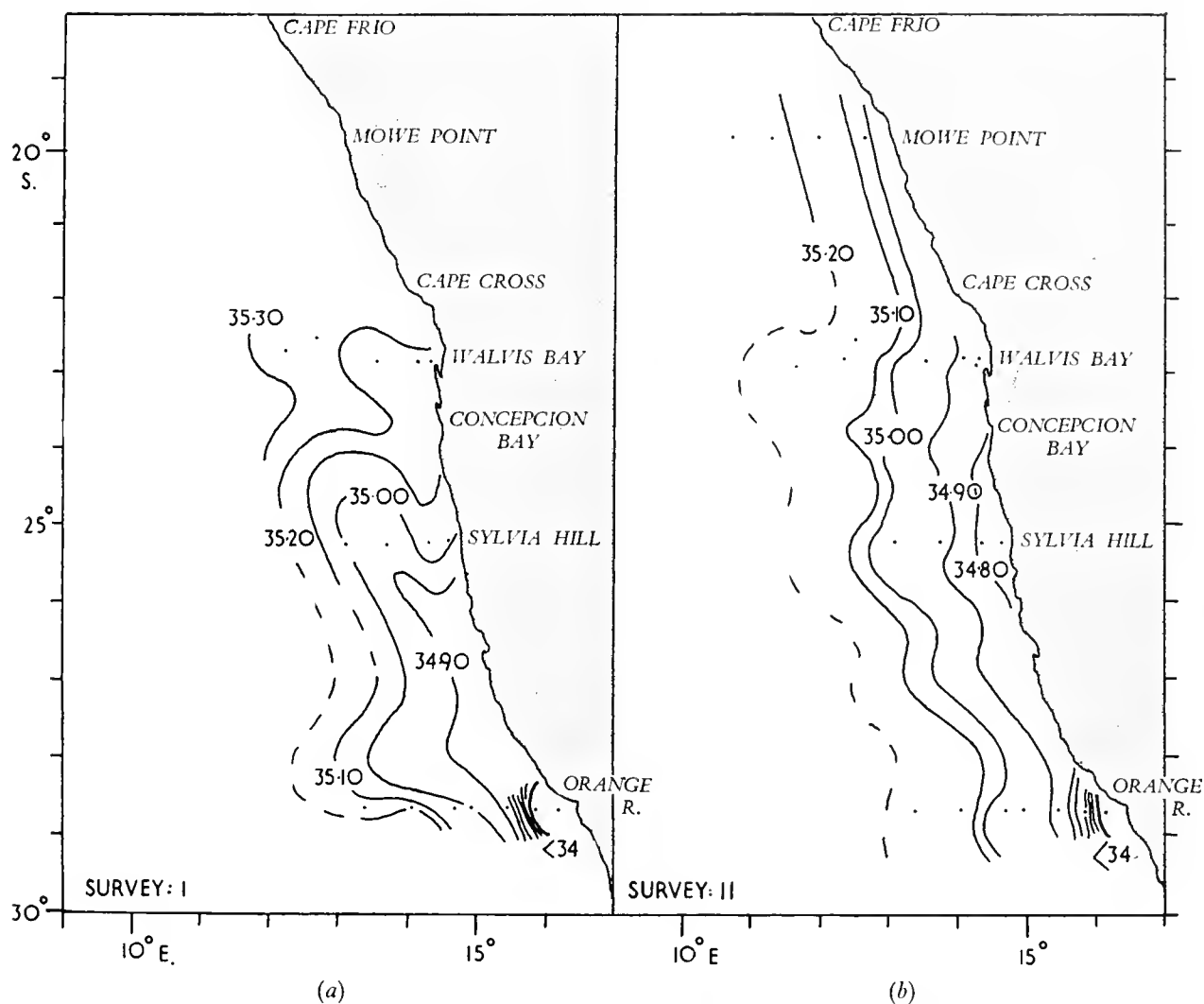
Fig. 8 (a). Distribution of surface-salinity (‰), survey I, March 1950. (b) Distribution of surface-salinity (‰), survey II, September–October 1950.

this system the cooler and less saline waters lay adjacent to the land, and the warmer, more saline waters farther offshore. Superimposed upon this distribution, however, there was a pronounced series of tongue-like formations within which the cooler coastal waters alternated with intrusions of the warmer oceanic waters lying to the west. Thus the cool waters were not in the form of a continuous belt along the coast, but rather were present as a series of isolated patches extending out from the coast and entering into eddies with the warmer oceanic waters. It will be shown, further, that within these eddies the cooler coastal waters were sharply separated from the warm oceanic surface-waters.

First survey (autumn)

Horizontal distribution of temperature and salinity

On the first survey the lowest surface-temperatures were found in the south of the region, off Paternoster Point (32° 40′ S.) where the lowest recorded was 12·5° C. This cold water, although we have no direct evidence, was probably confined to a fairly narrow coastal strip. In the vicinity of Cape of Good Hope the thermograph readings reached a value of 17° C. only 3 miles offshore, and so there is little likelihood that the cool water extended east of this point.
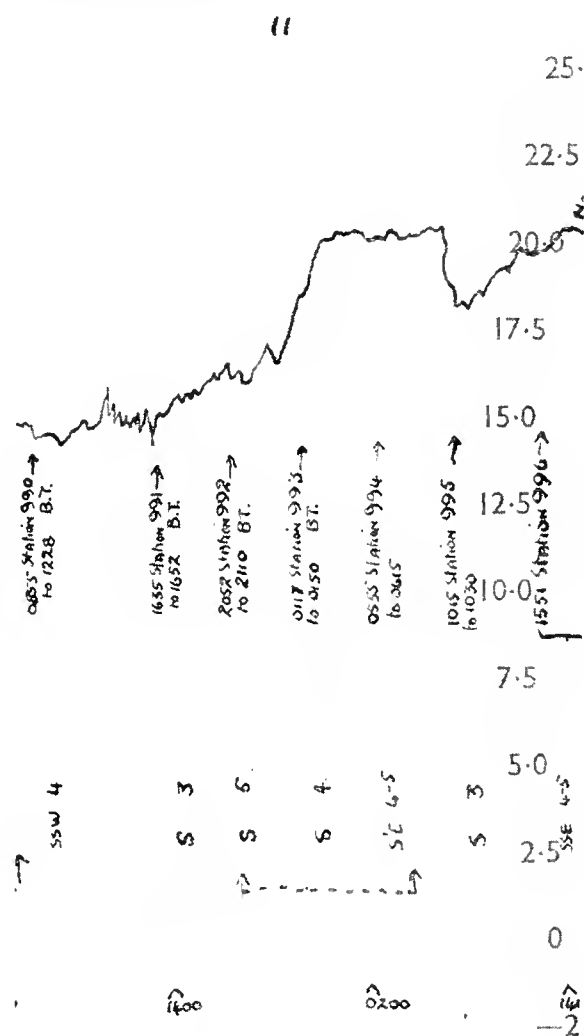
Fig. 9. Photograph of the annotated distant-reading thermograph chart for
Saturday, 11 March 1950. Vertical scale, temperature in ° C.

Northwards, towards the Orange river mouth, the extent of cool water became more restricted, and in 29° S. the warmer oceanic water penetrated more closely to the coast. The outflow of fresh water from the Orange river can be detected over a wide area. The surface-salinities at stations in the neighbourhood were vastly reduced (32·39‰ at WS 1001) but the reduction affected only a thin surface-layer, and 50 miles offshore at WS 1000 the surface-salinity was that of the normal sea-water of the region. To the west of station WS 998 the boundary with the warm oceanic water was sharply

defined by a sudden increase in both temperature and salinity (from 18·36 C., 35·01 ‰ to 20·18 C., 35·20‰).

The bathythermograph observations north of WS 996 show that the Orange river line of stations lay along the southern boundary of an extensive wedge of cool water, WS 955 marking its most westerly limit. To the north of this, typical oceanic temperatures were present at WS 994 and 993 but cooler water was again encountered at WS 992. The contouring of the isotherms shows these high surface-temperatures (WS 994, 993) as a tongue of oceanic water converging with the coast, and the strong temperature gradients on either side of it suggest that it was sharply discontinuous with the sur-
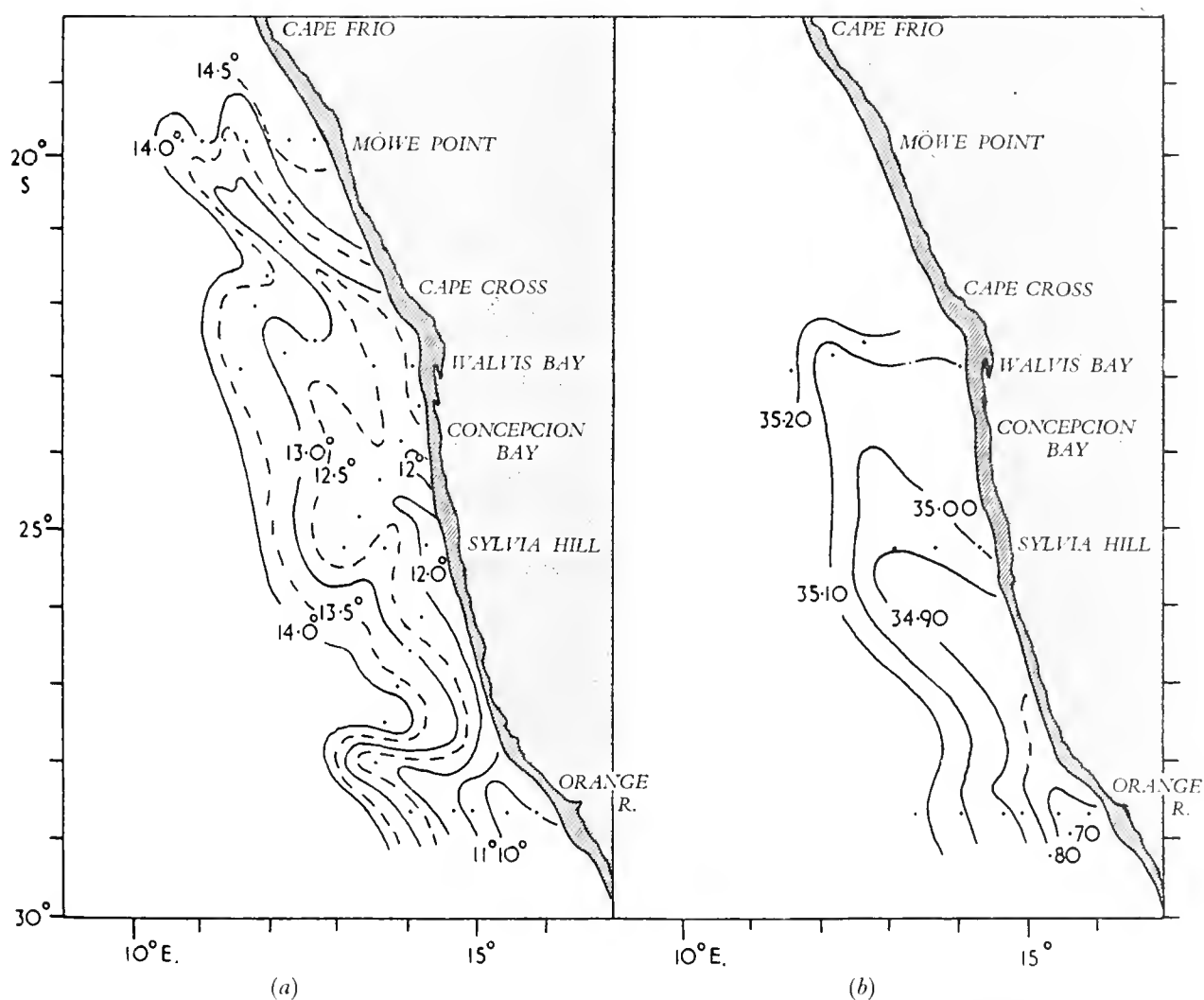
Fig. 10. Distribution of (a) temperature, and (b) salinity at a depth of 100 m., survey I, March 1950.

rounding cooler water; this is specially noticeable on its northern side, where the temperature fell 3·5° C. in about 15 miles at a distance of 60 miles west of Luderitz Bay (27° S.) (see Fig. 9).

On the next line of stations in 25° S. another such eddy can be defined, but here the oceanic water appeared to extend right in to the coast, causing the cooler water from the south to be displaced seawards. The increase to oceanic temperatures was not evident until WS 986, the westernmost station on the line. It may be that local heating of the surface-waters in the vicinity of station WS 988 had complicated the picture here, but the salinity at WS 988 was higher by 0·06‰ than at the next station seaward, not only at the surface but throughout the water column. A difference in salinity of this order of magnitude may not be significant in itself, but in conjunction with the temperature data

it strongly supports the hypothesis of an offshore influence at this point. Moreover the data to the north of this line also point to the presence of oceanic water converging southwards to this position.

Off Walvis Bay, and to the north of this warm wedge, the water was cooler again, but both the salinities and temperatures are higher than usual for the coastal water, the inshore values of 35·15‰ and 17° C. being more suggestive of some admixture between the two types of surface-water. At the western end of this line of stations, in 23° S., there was again a sudden increase of temperature and salinity into the northern boundary of the warm wedge, with temperatures of over 19° C. and salinities over 35.20‰.
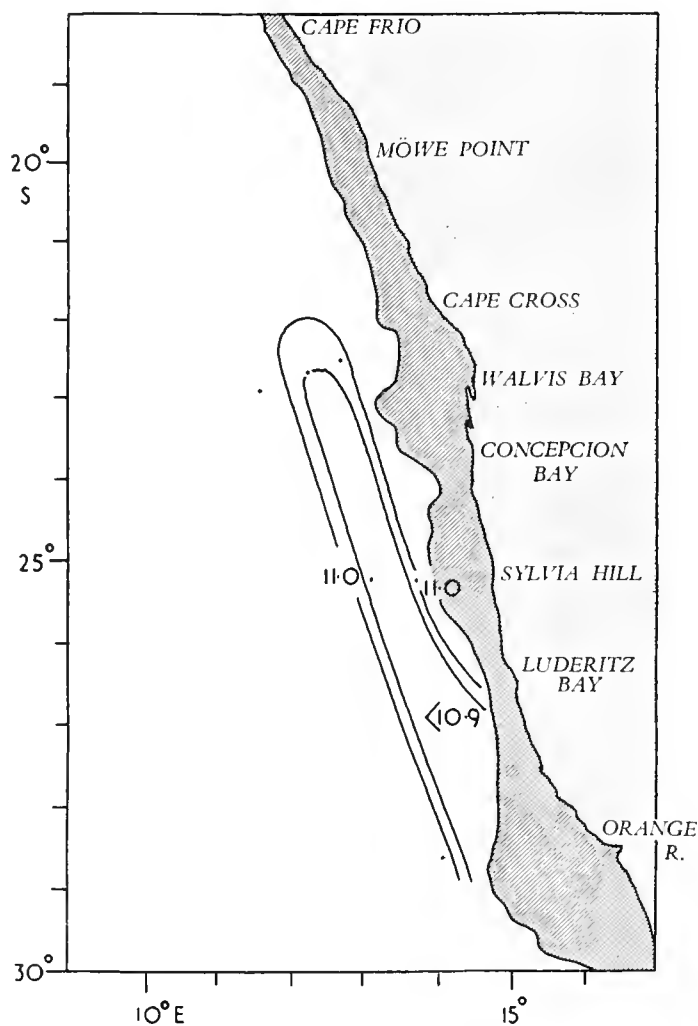
Fig. 11. Distribution of temperature at a depth of 200 m., survey I, March 1950.

To the north of 23° S. the oceanic waters extend in a thin surface-layer apparently pressing towards the coast between 22° and 20° S.

Along the coast the cooler water becomes more and more confined, and eventually to the north of 19° S it appears to converge strongly with the very warm offshore waters (> 22° C.) in a series of eddies about 25 miles from the coast. Finally all trace of it disappears in 16° S., where at 15 miles offshore a temperature of 26° C. was recorded. This whole region between 16° and 19° S. is typical of a convergence region, with very sharp and considerable variations of temperature. Probably the observations demonstrate a compression of the normal convergence between subtropical and tropical surface water, resulting from the presence along the coast of water so abnormally cool for such latitudes. This marked the northern limit of the upwelling region in March 1950.

At a depth of 20 m. the same general characteristics of the surface distribution are to be found, but by 50 m. a change is evident. The disposition of the isotherms and isohalines at these depths represents a transition in varying stages between the surface distribution and that at greater depths. The isotherms and isohalines at 100 m. (Fig. 10) exhibit some more considerable changes which are worthy of note. It will be seen that little change is evident in the Luderitz Bay–Orange river region, (27° to 30° S.) but the cooler coastal water can now be traced more continuously along the coast, and extends to the north in a tongue leaving the coast in the vicinity of Walvis Bay. On the landward flank of this extension warmer water is present, apparently intruding southwards along the coast as far as Concepcion Bay (24° S.). The eddy in 25° S. at stations WS 986 and 987 is still present, and from the north of it another area of low temperatures extends offshore through WS 977, with a markedly lower salinity (35·06‰) than the surrounding water at WS 976 and 978 (35·23‰ and 35·16‰ respectively).

The smaller number of observations made below this depth make it impossible to construct any detailed picture. It is evident, however, that at a depth of 200 m. (Fig. 11) there was an extensive area of cooler water extending N.N.W. from the area between Orange river and Luderitz Bay, the axis of this belt running through WS 986 and 977. Between this tongue and the coast the water was warmer and more saline and suggests a flow from the north along the edge of the continental shelf as far south as Luderitz Bay.

Vertical distribution of temperature and salinity

At most stations there is a layer of almost homogeneous water at the surface, within which the density remains almost constant with depth. This is generally referred to as the convection layer. Throughout the region it is present to a greater or lesser extent, and as a rule it is underlain by a

Table 5. *Depth of the convection layer*

Survey I		Survey II		Survey I		Survey II	
Station	Depth (m.)	Station	Depth (m.)	Station	Depth (m.)	Station	Depth (m.)
—	—	WS 1105	0	WS 982	4	WS 1074	10
—	—	WS 1104	0	WS 983	0	WS 1073	30
—	—	WS 1103	10	WS 984	0	WS 1072	30
				WS 985	4	WS 1071	10
WS 964	33	WS 1102	0				
WS 965	41	WS 1101	10	WS 986	0	WS 1070	30
WS 966	30	WS 1100	0	WS 987	0	WS 1069	0
WS 967	10	WS 1099	0	WS 988	0	WS 1064	0
WS 968	18	WS 1098	0	WS 989	0	WS 1063	0
WS 969	25	WS 1097	30				
WS 970	9	WS 1096	c	WS 990	10	WS 1062	0
				WS 991	0	WS 1061	10
WS 971	30	WS 1093	20	WS 992	9	WS 1060	10
WS 972	20	WS 1091	10	WS 993	30	WS 1059	50
WS 973	25	WS 1090	0	WS 994	40	WS 1058	100
WS 974	27	WS 1089	10	WS 995	5	WS 1057	100
WS 975	75	WS 1088	20				
				WS 996	10	WS 1056	50
WS 976	50	WS 1080	75	WS 997	10	WS 1055	50
WS 977	20	WS 1081	75	WS 998	20	WS 1054	30
WS 978	20	WS 1079	50	WS 999	10	WS 1053	10
WS 979	0	WS 1078	20	WS 1000	20	WS 1052	20
WS 980	0	WS 1077	30	WS 1001	0	WS 1051	10
WS 981	0	WS 1075	30	WS 1002	0	WS 1050	0

Where the depth figure 'o' occurs, it indicates that the convection layer was either absent or was less than 10 m. in thickness.

strong temperature discontinuity layer, through which the salinity remains almost constant. This discontinuity is therefore a layer of great stability.

The distribution and depth of the convection layer is set out in Table 5, zero indicating where none existed or where it was too thin to be recorded by our observations ($<$ 10 m).[1]

Comparing this table with the distribution of surface temperature and salinity (Figs. 7 and 8) it is clear that the convection layer is well developed in the oceanic surface-water, but is notably absent or ill defined in the cooler coastal waters, in which the temperature decreases more steadily from the surface to the sea-bed.

The Orange river line (28° 30′ S.). The vertical sections of temperature and salinity (Figs. 12 and 13) show that both the isotherms and isohalines trend upward to the coast. Although this pattern may suggest an active vertical uplift of water against the coast, such a movement does not appear likely in view of the well-developed discontinuity and the impoverished nature of the surface-waters (fig. 50). The great reduction in salinity of the surface-waters at the inshore stations has already been referred to, and the resulting decrease in density of the surface layers has led to very great stability at these stations.

It is suggested that this section shows an advanced stage of the upwelling process: a relic of previous upwelling rather than a stage of active uplift.

The Sylvia Hill line (25° S.) (Figs. 14 and 15). The whole water column at the inshore stations, WS 988 and 989, was very stable. Clearly there is no indication of inshore upwelling on this line, but then it will be remembered (p. 160) that the inshore stations were apparently influenced by a convergent tongue of oceanic water from the north, and that the cooler water had been displaced offshore. In this cooler water the lower stability and patterns of the isohalines in particular are strongly indicative of vertical motion at stations WS 986 and 987.

The Walvis Bay line (23° S.) (Figs. 16 and 17). The salinity section shows a prominent tongue of highly saline water near the surface. Within this the temperatures are high, and it is characterized by a pronounced thermal discontinuity. This is the northern edge of the intrusion of oceanic water which curves to the south and influences the inshore station on the preceding line. On this Walvis section the discontinuity remains well marked at the inshore stations, and the relatively high temperature and salinity of the latter show that no active upwelling was in evidence. The nature of the inshore water masses here is somewhat problematical, for they appear to exhibit characteristics of a mixture of the oceanic and coastal waters. The most plausible interpretation is that previously upwelled water has subsequently become mixed with oceanic water and the resultant mixture occupies the area in the proximity of the coast at Walvis Bay.

The Möwe Point line (19° 44′ S.). Extending throughout the area to the north of Walvis Bay the oceanic surface-waters form a thin layer about 50 m. deep, overlying a very strong temperature discontinuity. A section through this layer is shown in Fig. 18, which shows the most northern line of stations (the Möwe Point line). It will be seen that on the inshore boundary of this layer the discontinuity weakens and slightly cooler water lies against the coast. Although no salinities were taken in this region it is highly probable that the coastal water is again an admixture of the oceanic and coastal water types. There is a slight indication that the upward trend of the isotherms towards the coast may represent a very early stage of upwelling.

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[1] No salinity observations have been available for the 'bathythermograph stations', and so certain assumptions have been necessary. At all full stations the character of the upper layer density distribution, and consequently the convection layer, was primarily dependent upon variations of temperature, and the slight variations of salinity have affected the density curves only slightly. It has therefore been considered justifiable to define the convection layer from the temperature curves at the bathythermograph stations, as the layer within which the temperature remained almost constant.

Fig. 12. Distribution of temperature (° C.). Section off the mouth of the Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.

Fig. 13. Distribution of salinity (‰). Section off the mouth of the Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.

At all of the stations below the discontinuity layer the temperature and salinity decrease with depth towards the core of the antarctic intermediate water.

This outline of the conditions on the first survey leads us to the conclusion that, in the region surveyed, two principal types of surface-water can be identified.

(*a*) The coastal or upwelled water, with a low salinity of 35·00‰ or less, and low temperature < 18·0° C., and as a rule without any marked convection layer.
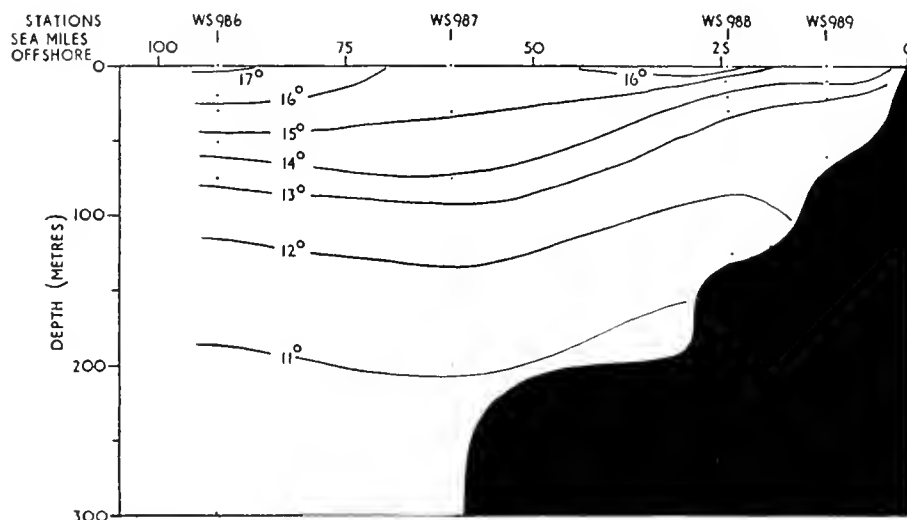
Fig. 14. Distribution of temperature (° C.). Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of the stations are shown in Fig. 1.
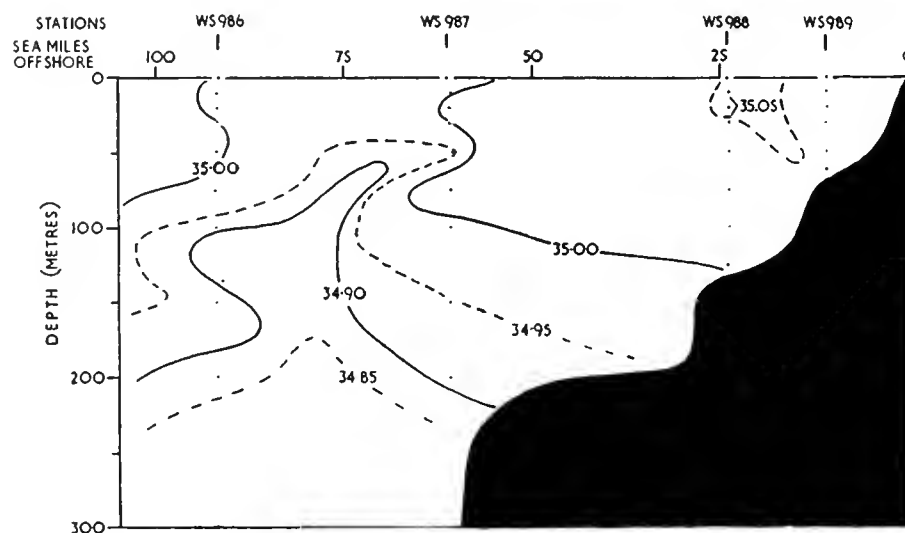
Fig. 15. Distribution of salinity (‰). Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of the stations are shown in Fig. 1.

(*b*) The offshore or oceanic water with a high temperature, usually > 18° C., high salinity > 35·20‰ and a well-developed convection layer.

It is evident that mixtures of these waters occur, as was found in the vicinity of Walvis Bay, but generally they are found sharply distinguished from one another with a pronounced boundary.

There is also evidence of considerable surface heating having affected the coastal waters on survey I, and along with the lack of evidence of active upwelling, this suggests that the conditions throughout the area represent a quiescent state subsequent to previous upwelling.
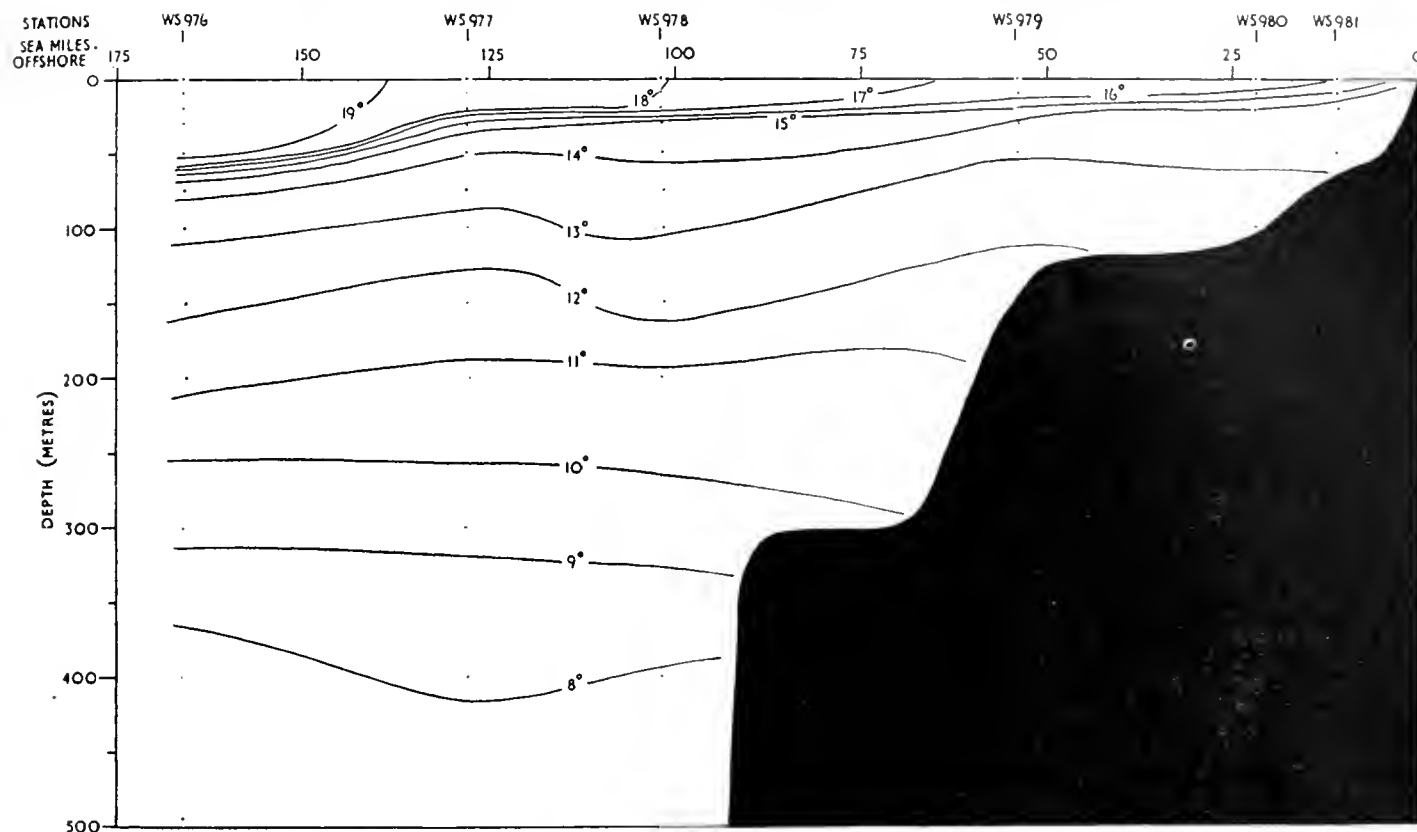
Fig. 16. Distribution of temperature (° C.). Section off Walvis Bay, 6–8 March 1950, survey I.
Positions of stations are shown in Fig. 1.
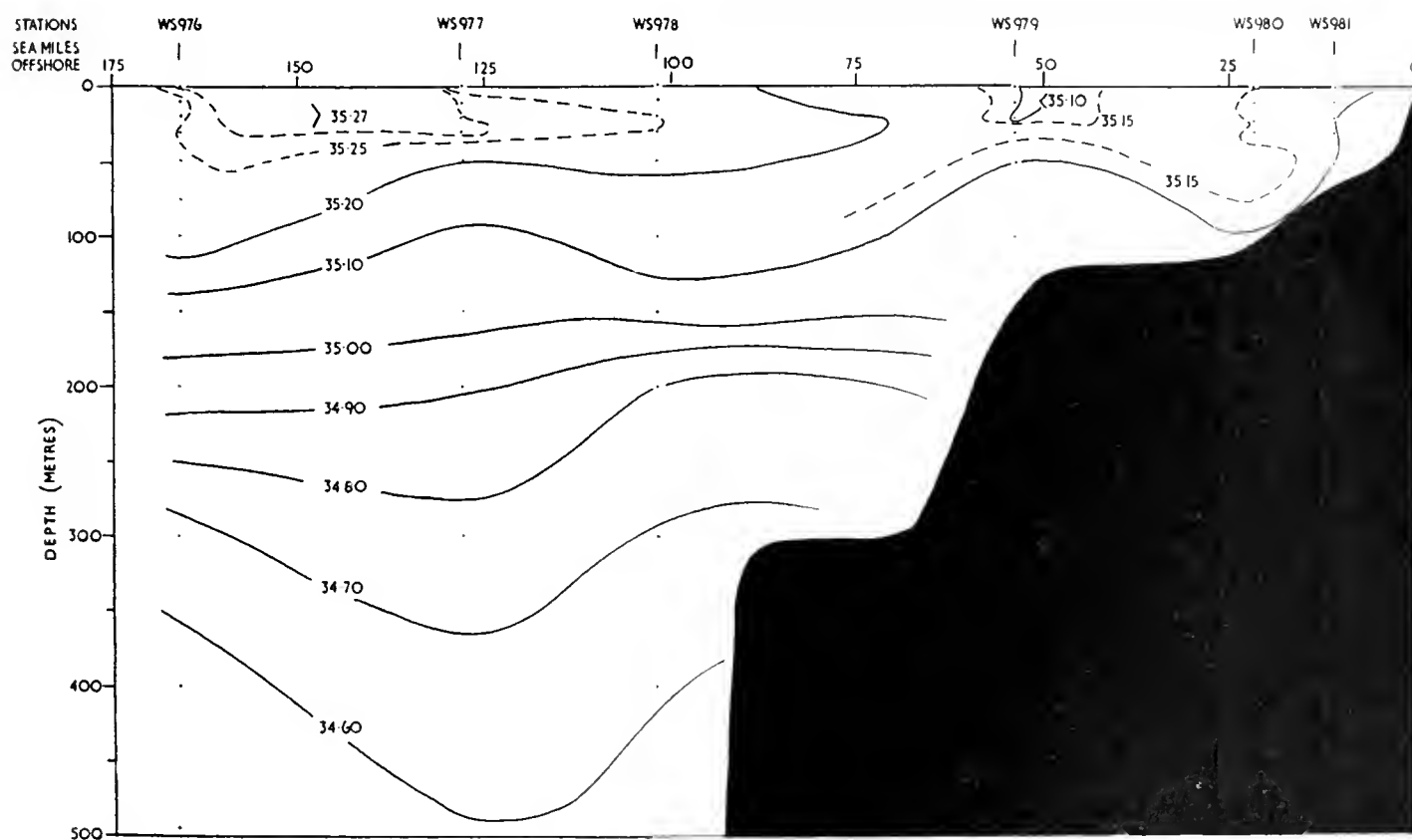
Fig. 17. Distribution of salinity (‰). Section off Walvis Bay, 6–8 March 1950, survey I.
Positions of stations are shown in Fig. 1.
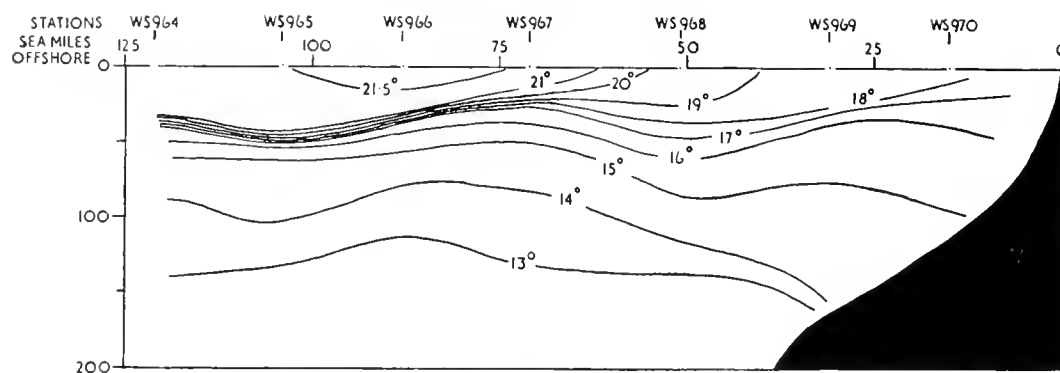
Fig. 18. Distribution of temperature (° C.). Section off Möwe Point, 4–5 March 1950, survey I. Constructed from bathythermograph observations, the positions of which are shown on Fig. 1.

Second survey (spring)

Horizontal distribution of temperature and salinity

On survey II the trend of the surface isotherms and isohalines was similar to that on survey I, but throughout the whole region the temperatures were markedly lower. This can to a large extent be attributed to the seasonal change, survey II having taken place about the coolest time of the year; but also, as will be shown in what follows, the more active upwelling before and during this survey has also contributed to the overall effect.
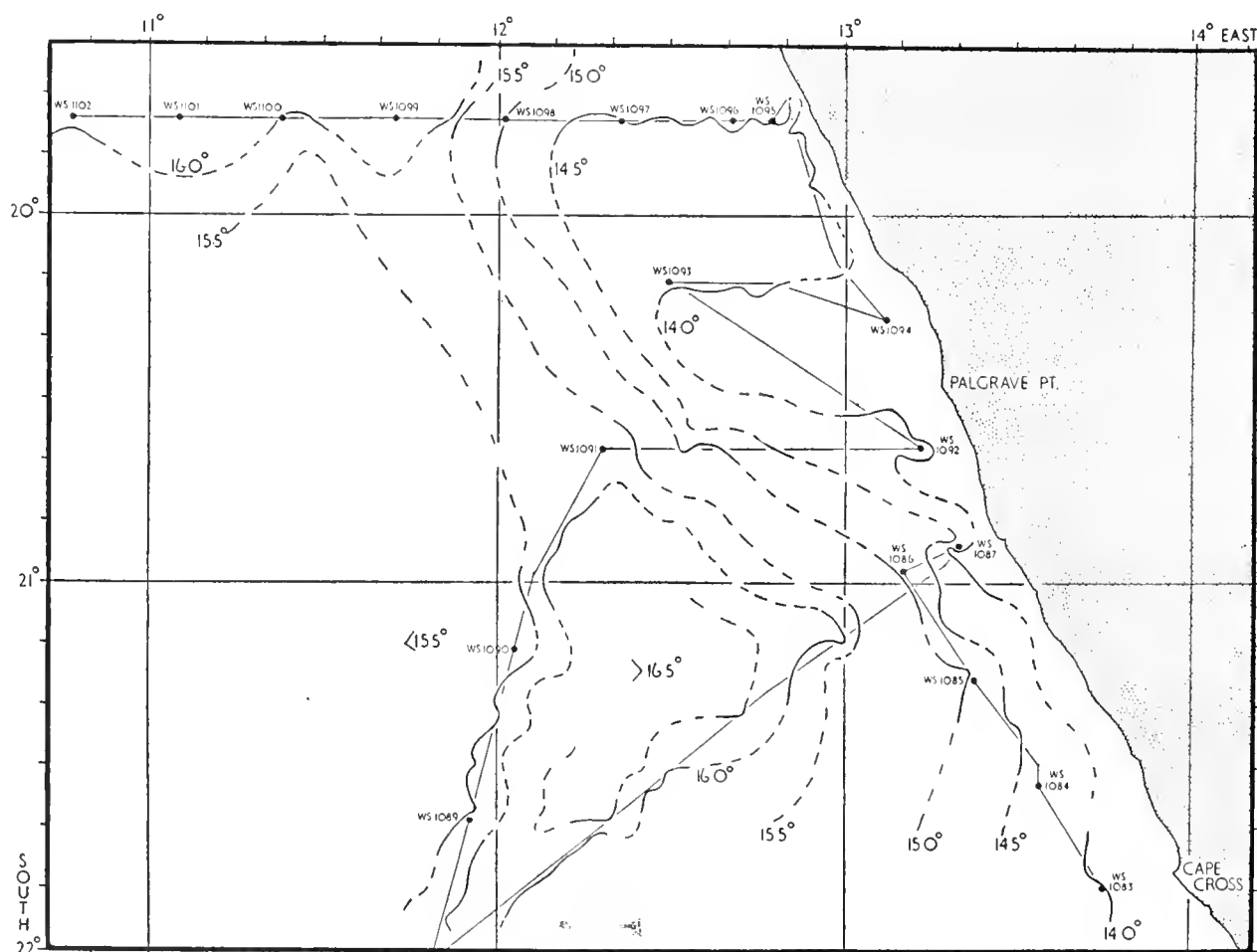
Fig. 19. Distribution of surface-temperature (° C.) between Cape Cross and Möwe Point, survey II, constructed from station observations and distant-reading thermograph records. The track of the ship between stations is shown by the thin line.

The lowest surface-temperature recorded (Fig. 7b) was 10° C., off the mouth of the Orange river, but all along the coast as far south as the Cape of Good Hope the temperatures remained below 13° C. In 31° to 32° S. oceanic water with a temperature of 15° C. approached more closely to the coast, but to the north of this the coastal water extended far seawards, forming a broad tongue with its axis extending westwards in 29° S.

In contrast to survey I the Orange river line of stations, which occupied the same positions on both surveys, lay on the northward side of this tongue of colder water. To the north of these stations oceanic water again intruded towards the coast in 28° S. The low salinities in the vicinity of the
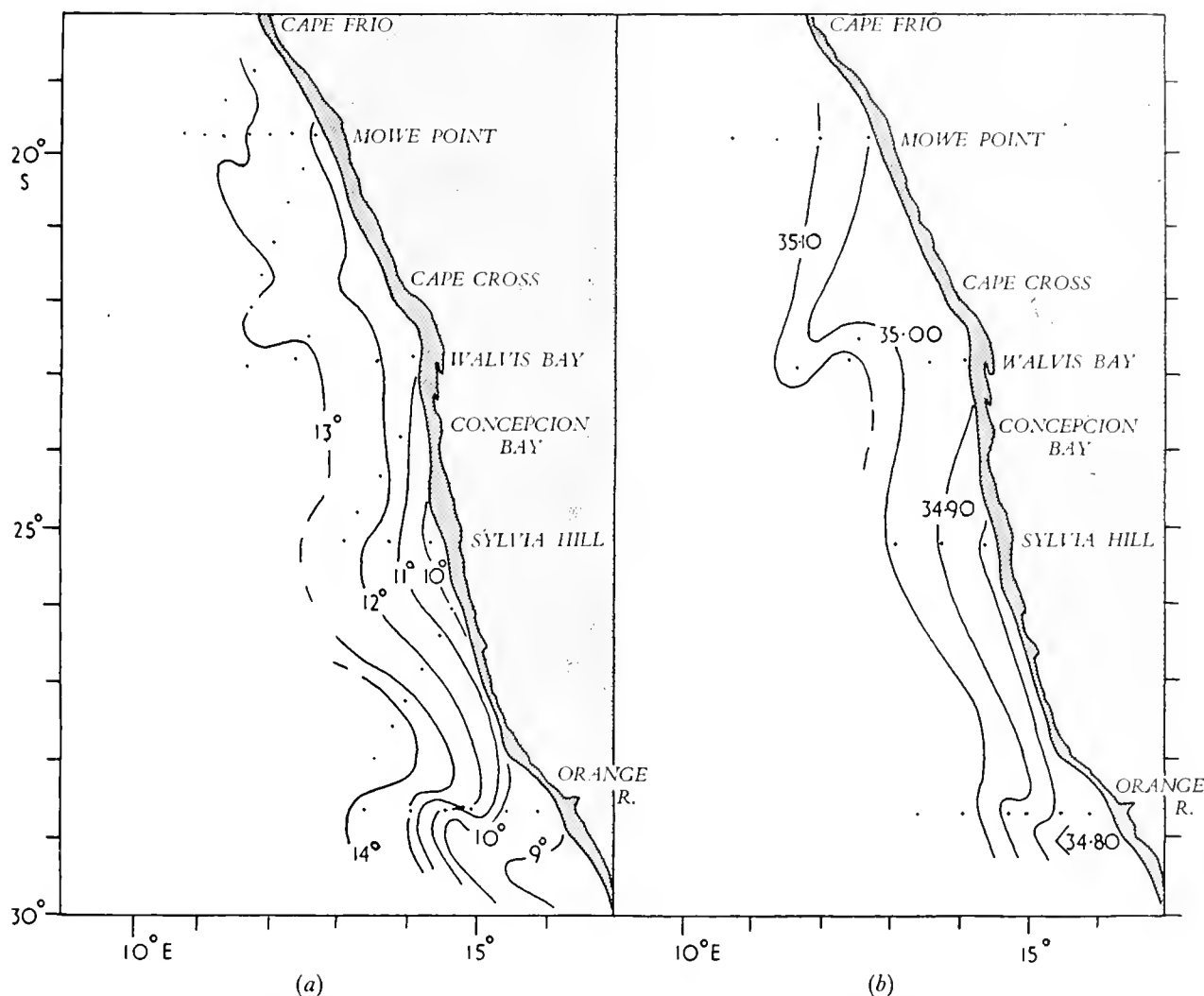
Fig. 20. The distribution of (a) temperature (° C.), and (b) salinity (‰) at a depth of 100 m. on survey II, September–October 1950.

Orange river mouth were again evident. A sudden increase in salinity between stations WS 1054 and 1055 marked the boundary of coastal and oceanic waters.

Another sharp boundary was traversed between stations WS 1059 and 1060 on the northern side of the oceanic water.

To the north of 27° S. the cooler waters became very extensive, and up to Walvis Bay in 23° S. there was a complex series of small eddies formed by the cooler water, apparently driving offshore in a north-westerly direction. Throughout this area sharp fluctuations of sea temperature were continually encountered, but the temperature remained consistently low.

The stations at the inshore end of the Walvis Bay line all show the typical features of the cool coastal waters, with temperatures of less than 13° C. and salinities of less than 35·00‰. The stations at the offshore end of the line, on the other hand, lying in warmer and more saline water, are characteristic of oceanic conditions. (It should be noted here that the contouring of the isotherms at WS 1079–81 may be open to question for the observations at WS 1079 were taken before, and those at WS 1080 and 1081 after, a considerable gale. As will be shown later (p. 188) this gale produced a considerable alteration in the position of the surface isotherms, and yet no allowance could well be made for this in the general picture).
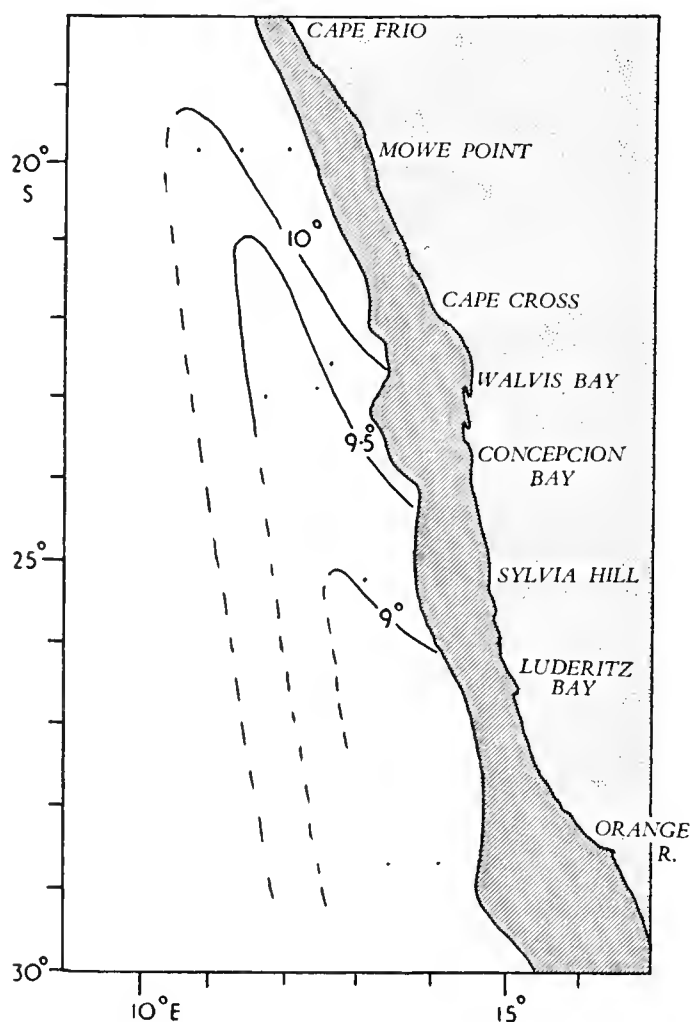
Fig. 21. The distribution of temperature (° C.) at a depth of 300 m. on survey II, September–October 1950.

Between the Walvis Bay line and the Möwe Point line the distribution of surface-temperature is exceedingly complex. From the bathythermograph observations and the records from the distant reading thermograph a more detailed construction of the surface isotherms has been set out in Fig. 19. It will be seen that while the cool coastal water (less than 14° C.) continues along the coast as far as Möwe Point, the temperature rises fairly rapidly offshore to an area of relatively high temperature some 60 miles from the coast. Here the temperature is typically oceanic, reaching a recorded maximum of 16·5° C. This area of high temperature, a patch about 60 miles in diameter, is apparently an isolated feature, for on its western boundary the temperature is again lower (15·5° C.) Several interpretations could be made of this distribution, and unfortunately little guidance can be obtained from the sub-surface data, which are only available at the stations. It may be that this phenomenon is solely due

to local surface-heating, but on the other hand the bathythermograph observations definitely suggest, although not conclusively, that this feature is part of an extensive detached eddy between 'oceanic' and 'coastal' types of water. If this interpretation is correct the cooler water outside this warm area would combine to give the eddy an overall diameter of some 120 miles, and extending in depth to 50 m.

At Cape Frio, in 18° 30' S., a temperature of 15·1° C. was recorded about 7 miles offshore, but north of this yet another patch of cooler water was present, extending up to the Cunene river mouth. From there northwards, however, the temperature of the surface-waters increased steadily, until in 14° S. the tropical boundary was encountered and the temperature increased rapidly to values over 22° C.

The distribution of temperature and salinity at a depth of 100 m. (Fig. 20) has the same general characteristics as that at the surface, the cooler and less saline waters lying uniformly along the coast, with the warmer more saline waters offshore. Although the smaller number of observations at this depth are probably responsible for the smoothing out of the isotherms and isohalines, they still show up quite clearly the pronounced eddy in the vicinity of the Orange river. The regions of lowest temperature and salinity as shown by the 10·0° C. and 34·80‰ isolines are present to the south of the Orange river and off Luderitz Bay.

At 150 m. an entirely different pattern appears. This is not illustrated but along with the distribution at 200 m. it represents a transition to the distribution at 300 m. (Fig. 21). At 300 m., in spite of the paucity of observations, it is possible to recognize that the distribution is roughly similar to that at a depth of 200 m. on survey I. Here we find an apparently anomalous situation with the warmer and more saline water nearest to the coast while the cooler water lies further offshore. There can be no doubt that further to the west warmer water must have been present, and so it seems that on this survey the cooler water at this depth must have been still more extensive and further displaced from the shore than on survey I. This was concurrent with an increase in the current of warmer water which runs south along the coast.

Vertical distribution of temperature and salinity

An outstanding feature of the second survey in comparison with the first is the absence of the very strong thermoclines which were found so frequently in March. At most stations, particularly those in the offshore waters, there is a convection layer on the surface, and below this the temperature and salinity decrease gradually into the deeper water. In several places where a well-defined convection layer had apparently been present, surface heating has reduced the density and produced a thin stable surface layer. The depth distribution of the convection layer on survey II is shown in Table 5.

The Orange river line (28° 30' S.). The low surface salinities inshore are a result of the fresh-water inflow of the river, and they have produced a very stable surface layer at station WS 1050. Further offshore, however, at WS 1051 a thin convection layer is present, and this deepens and becomes more pronounced farther to the west. The vertical sections of temperature and salinity (Figs. 22 and 23) contrast vividly with the conditions in March. The marked upward slope of the isotherms and isohalines towards the coast, combined with the active offshore transport of surface-water as suggested by the salinity section, shows most clearly the characteristics of active upwelling. It will also be seen that the isotherms and isohalines, while approaching the surface inshore, also rise towards the surface in the proximity of the edge of the continental shelf. There seems to be clear indication, therefore, of an additional divergent movement in this position. As will be shown later, this is probably associated with the mechanism of the process of the upwelling.

North of the Orange river line the tongue of warm offshore water at WS 1057 and 1058 has an almost constant temperature in the upper 100 m. A relatively sharp boundary was present on the
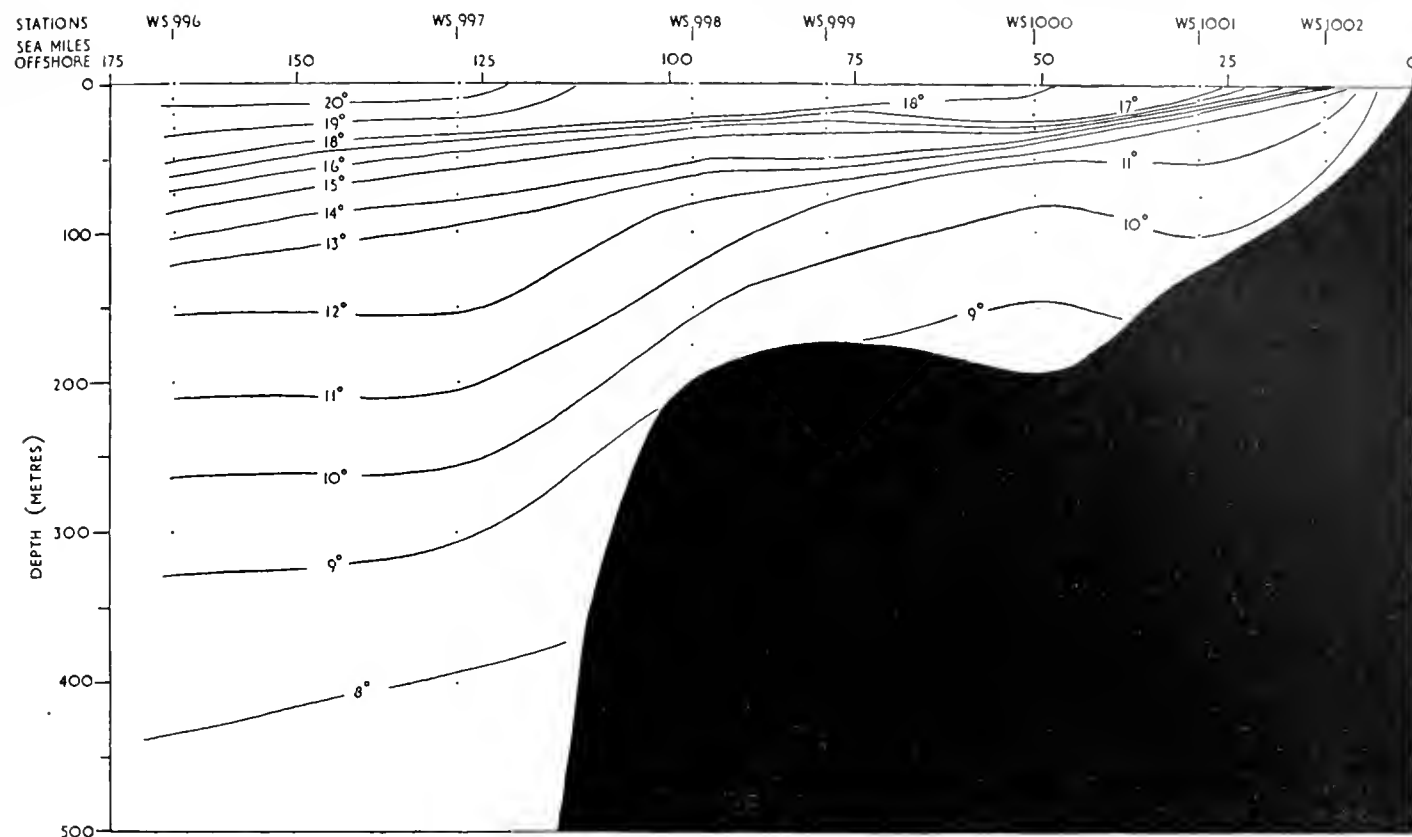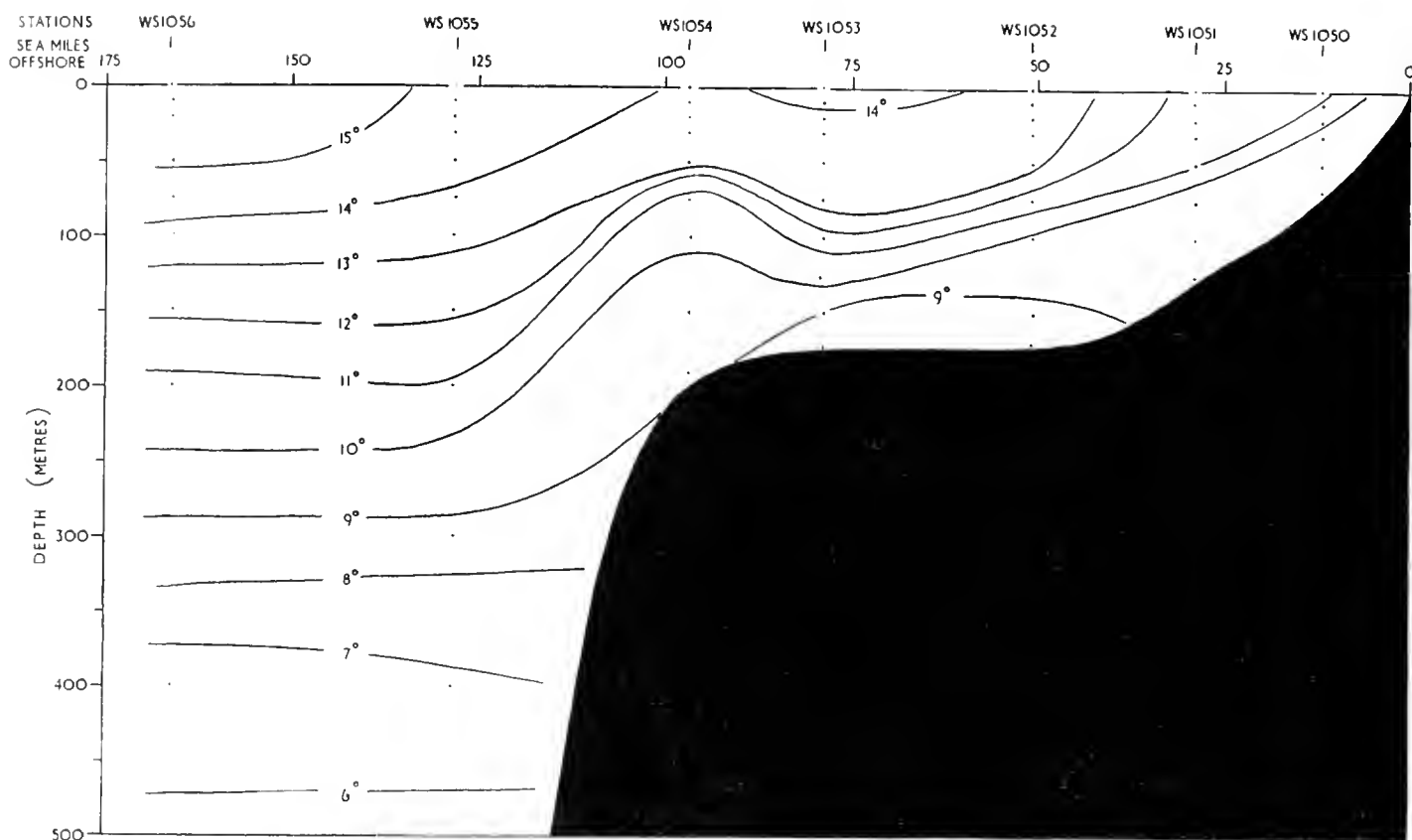
Fig. 22. Distribution of temperature (° C.). Section off the mouth of the Orange river, 21–24 September 1950, survey II. Positions of the stations are shown in Fig. 2.
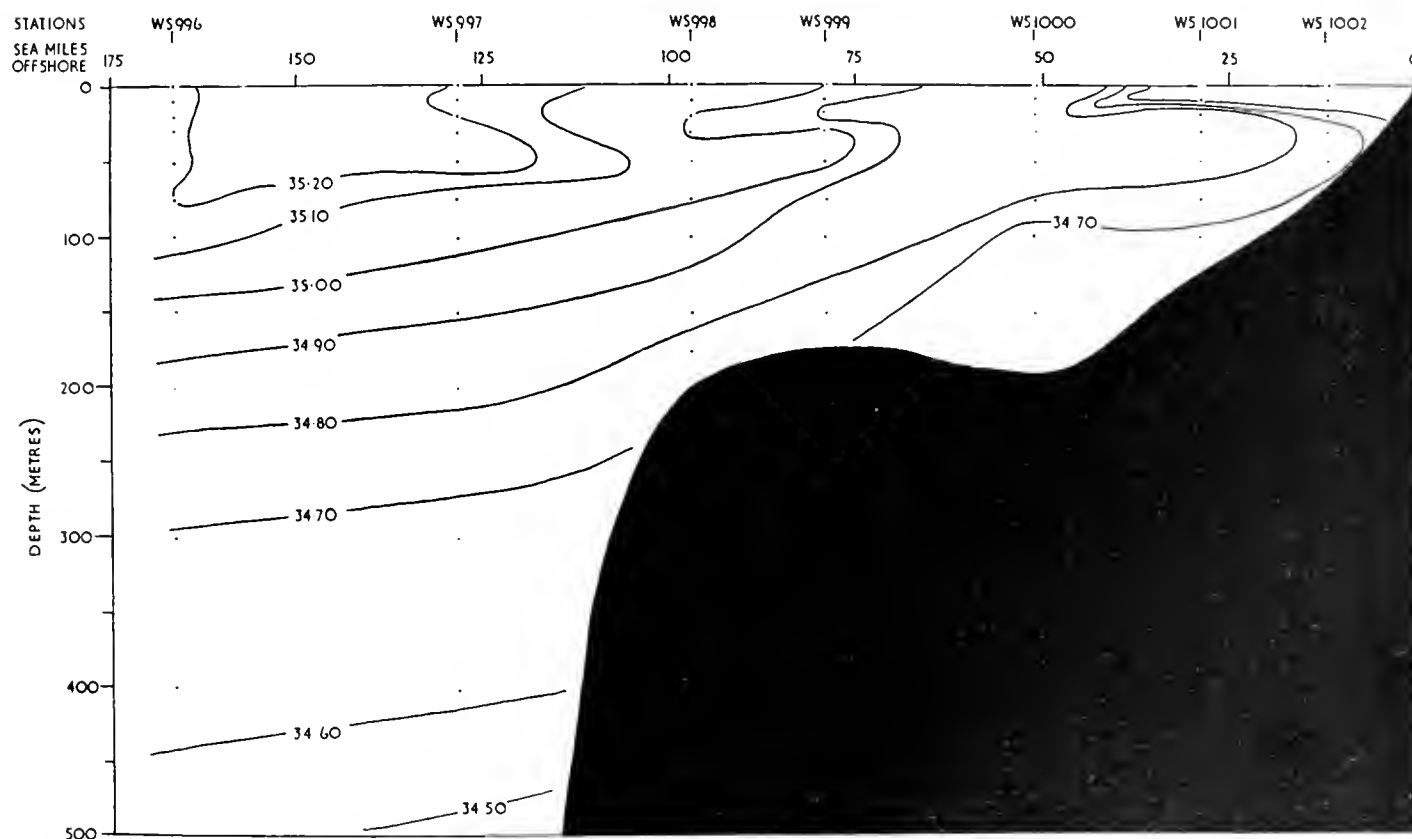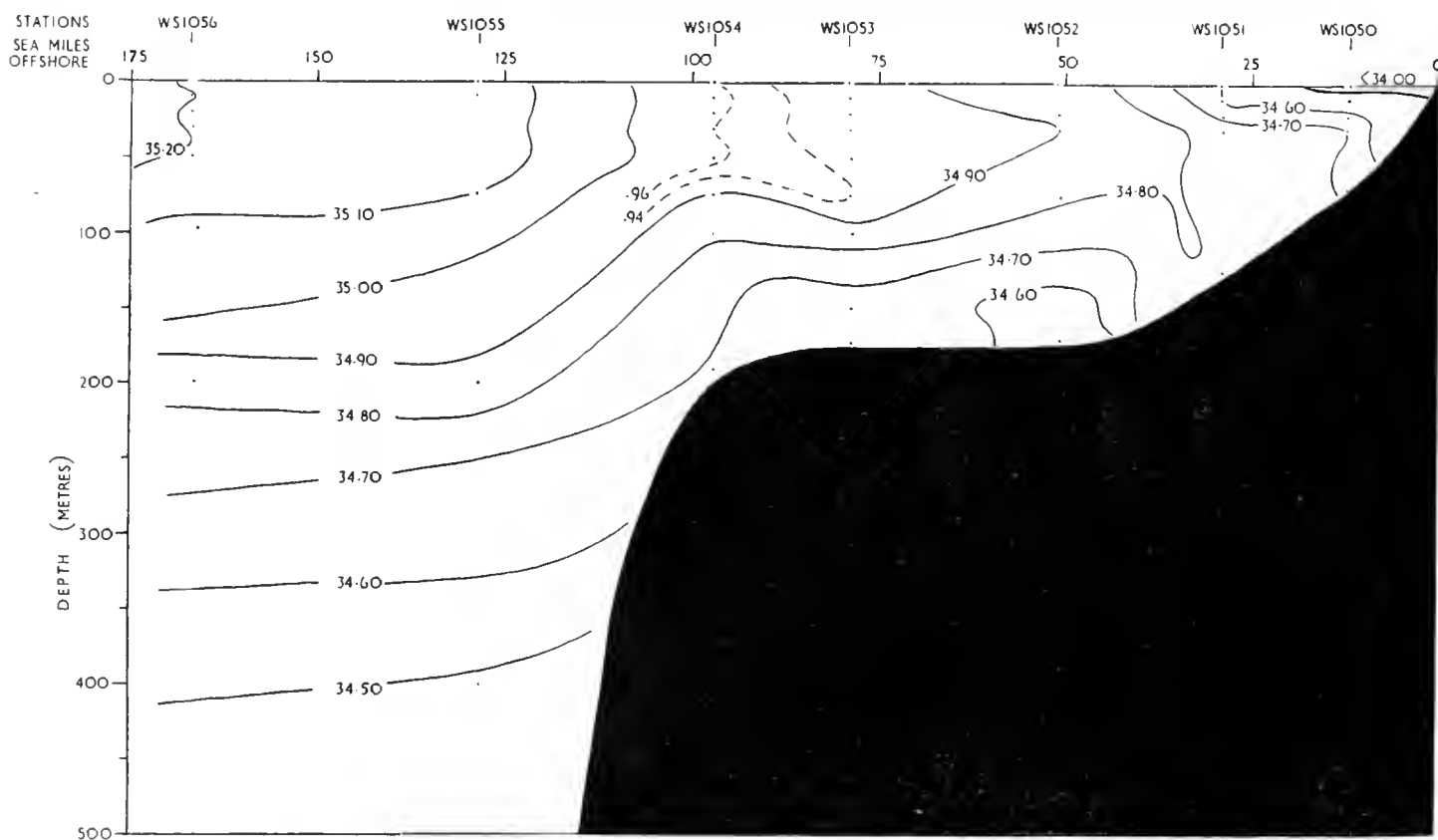

Fig. 23. Distribution of salinity (‰). Section off the mouth of the Orange river, 21–24 September 1950, survey II. Positions of the stations are shown in Fig. 2.

northern side of this wedge, where it abutted on the cooler coastal water. At stations WS 1061 and 1062 a slight temperature inversion was revealed by the bathythermograph observations, at depths of 105 and 75 m. respectively (Fig. 24).

The Sylvia Hill line (25° S.). Stations WS 1063–70 did not lie sufficiently far to the west to reach the boundary with oceanic water, and consequently they all lie within the coastal water. The vertical sections (Figs. 25 and 26) show that active upwelling must have been taking place on this line.

The Walvis Bay line (23° S.). Here again there are indications of active upwelling (Figs. 27 and 28). The inshore waters show an interesting point: the salinity of the inshore surface-water is very low (34·84‰) and remained low out to WS 1078 (34·96‰). Below this, however, the salinity increased to 34·97‰ on the sea bed of the continental shelf.

The salinity section suggests that there is a pronounced uplift of deeper water taking place on the edge of the continental
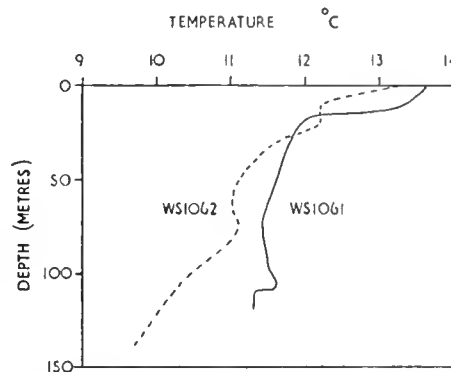
Fig. 24. Graph of temperature (° C.) against depth (metres) at stations WS 1061 and 1062, showing inversions present at these stations.
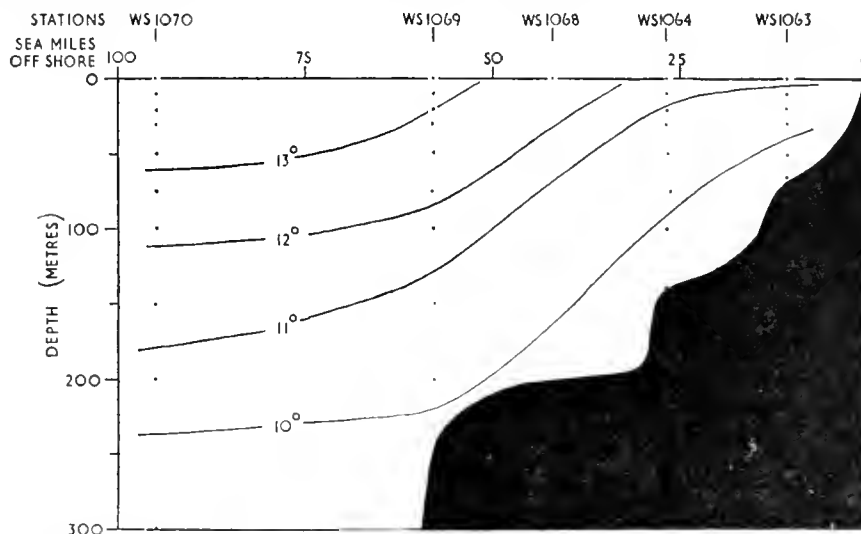
Fig. 25. Distributions of temperature (° C.). Section off Sylvia Hill, 25–27 September 1950, survey II. Positions of the stations are shown in Fig. 2.
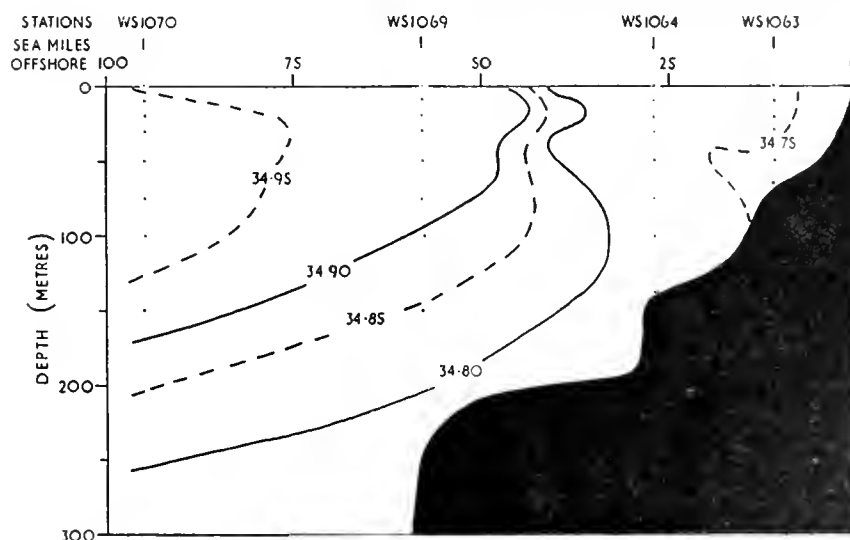
Fig. 26. Distribution of salinity (‰). Section off Sylvia Hill, 25–27 September 1950, survey II. Positions of the stations are shown in Fig. 2.
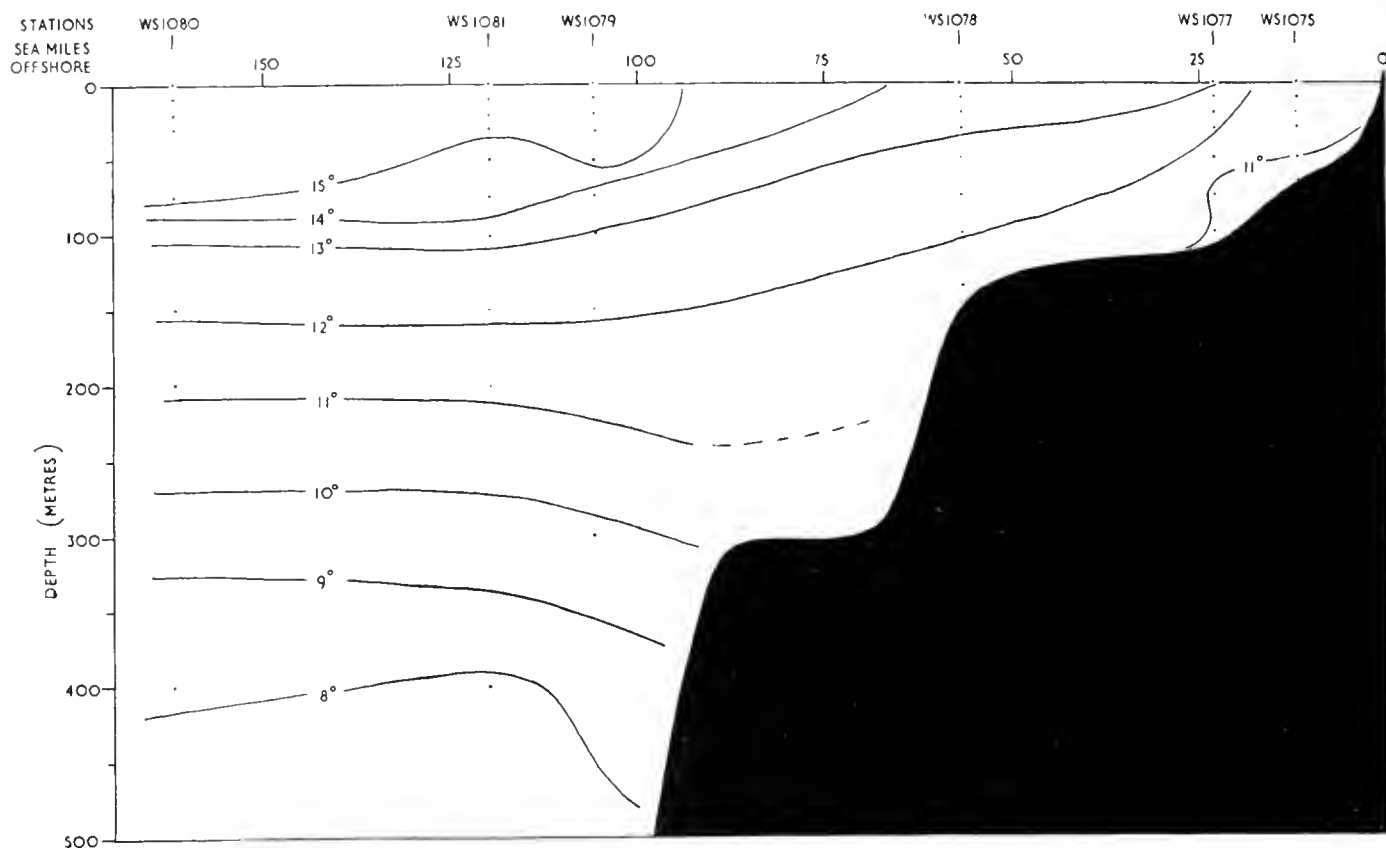
Fig. 27. Distribution of temperature (° C.). Section off Walvis Bay, 29 September–3 October 1950,
survey II. Positions of the stations are shown in Fig. 2.
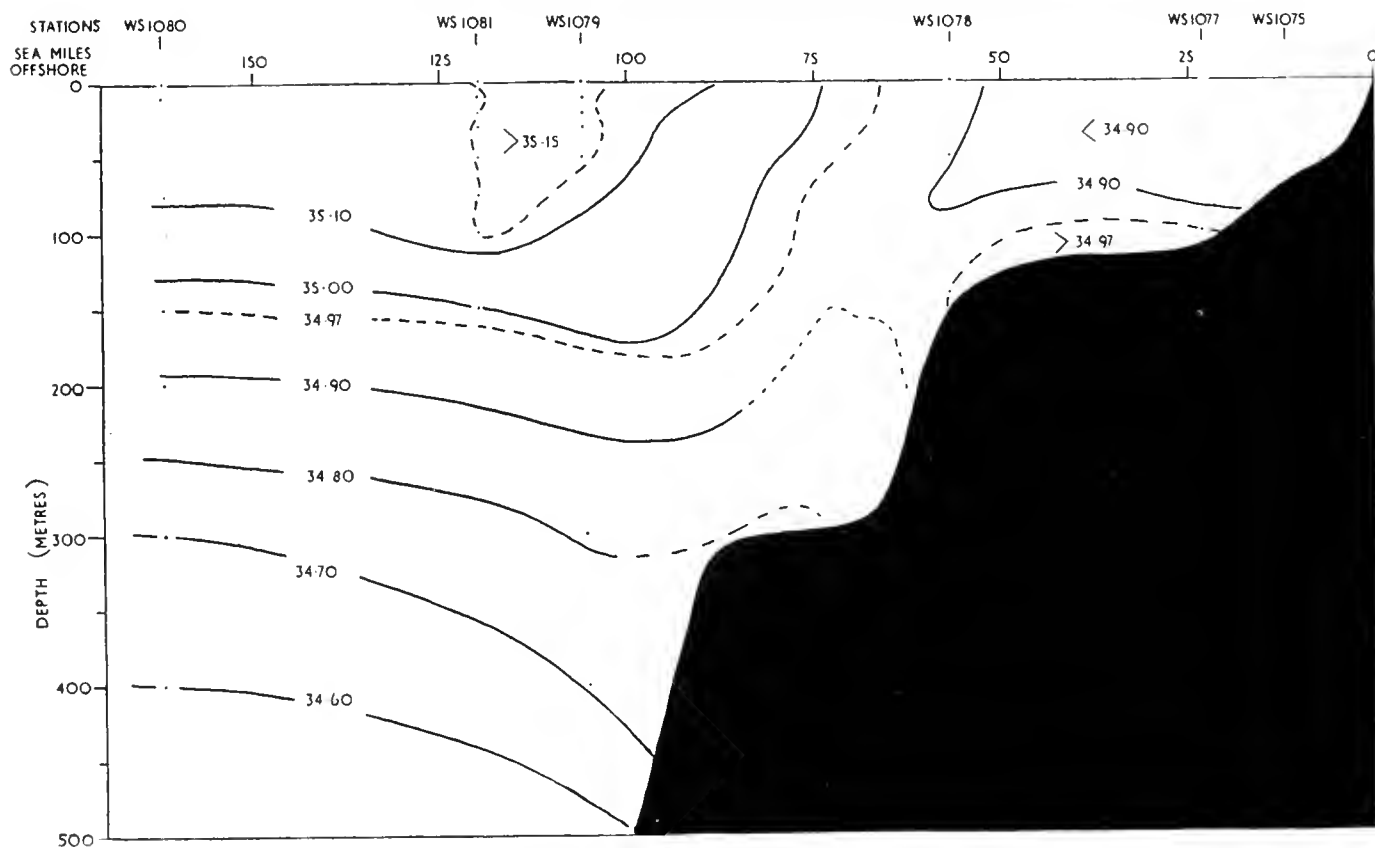
Fig. 28. Distribution of salinity (‰). Section off Walvis Bay, 29 September–3 October 1950, survey II.
Positions of the stations are shown in Fig. 2.

shelf, and that the low salinity of the surface-layers inshore must be connected with this movement, but it is difficult to interpret the significance of such a movement.

The lack of any salinity observation in the region of the large eddy between the Walvis Bay line and the Möwe Point line prevents us from drawing any conclusion about the structure and movement of these waters.

The Möwe Point line (19° 44′ S.) (Figs. 29 and 30). Throughout the greater part of this line the
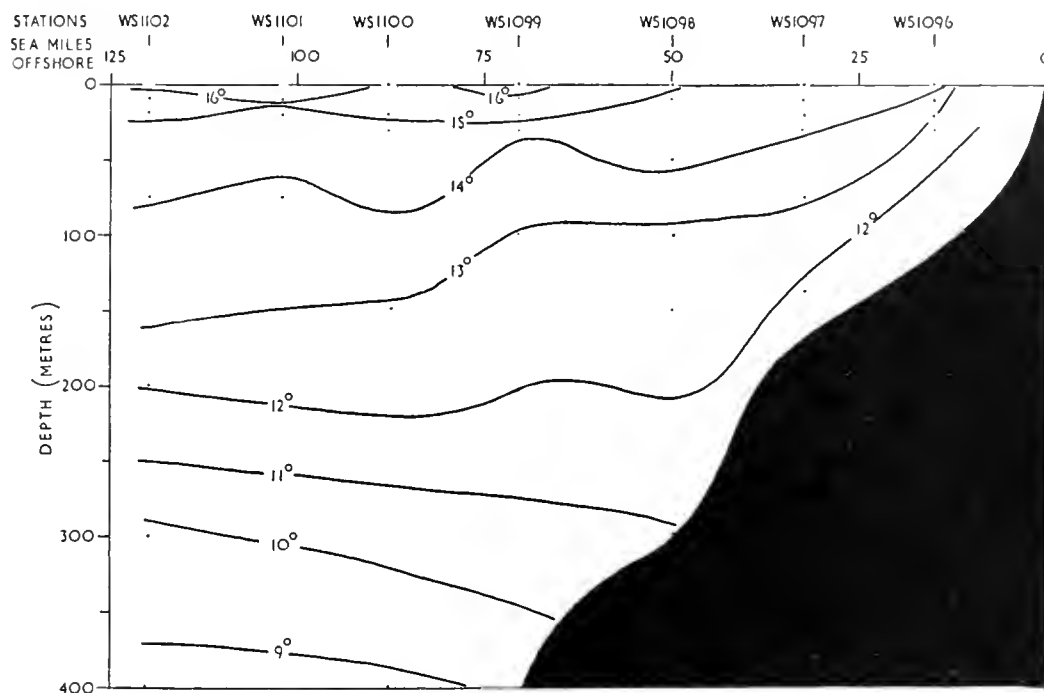
Fig. 29. Distribution of temperature (° C.). Section off Möwe Point, 9–11 October 1950, survey II. Positions of the stations are shown in Fig. 2.
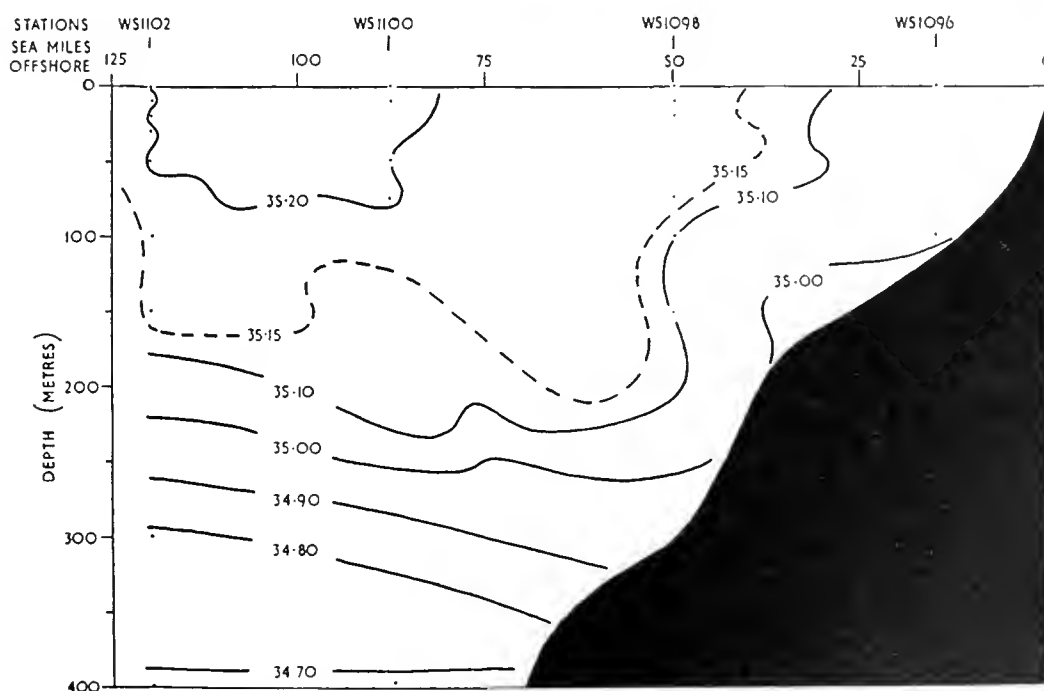
Fig. 30. Distribution of salinity (‰). Section off Möwe Point, 9–11 October 1950, survey II. Positions of the stations are shown in Fig. 2.

highly saline water at the surface, bounded both inshore and offshore by water of lower salinity, shows that the stations have sectioned the northern edge of oceanic surface-water which was involved in the large eddy lying south of this line. The isotherms and isohalines both slope upwards towards the coast at the inshore stations, but this does not necessarily mean that active upwelling was taking place. The same effect could be created by the presence of the oceanic water so close to the coast, compressing the coastal type of water into a narrow strip adjacent to the land. The salinity and temperature distribution in such a strip of water would then necessarily, on account of the laws governing the density distribution, resemble the pattern created by upwelling.

The isolation of this inshore water from the deeper water, apparent in the salinity section (Fig. 30), suggests that active upwelling was not taking place.

To the north of this section another centre of upwelling may have been present at Cape Frio (see Fig. 7b) in 18° 30' S., but there are insufficient data to decide this question.

To sum up, it is evident that the same essential features were present on both of these surveys. On the second survey we can distinguish the same two types of surface water.

(a) The coastal or upwelled water, which on survey II is characterized by temperatures below 14·0° C. and salinities of less than 35·00‰. The convection layer in this water is better developed than on survey I, but the underlying discontinuities are not so pronounced. These differences must be caused by the stronger winds and upwelling on survey II.

(b) The offshore water, characterized by temperature over 14·0° C. and salinities of over 35·10‰. This is in general cooler, but very similar in other respects to the same type of water on survey I.

In survey II, active upwelling was found on the two southern sections, and possibly also on the Walvis Bay line, while only on the northernmost section (the Möwe Point line) were quiescent conditions encountered.

Table 6. *Stability of the* 0–50 m. *and* 0–100 m. *layers*

	Survey I			Survey II	
	$10^5 \, d\sigma t/dz$			$10^5 \, d\sigma t/dz$	
Station	*0–50 m.*	*0–100 m.*	*Station*	*0–50 m.*	*0–100 m.*
WS 976	−63	845	WS 1102	975	743
WS 977	2000	1453	WS 1100	675	550
WS 978	2113	1535	WS 1098	500	495
WS 979	1825	1297	WS 1096	1213	855
WS 980	2050	1387			
WS 981	1775	—	WS 1080	63	268
			WS 1081	388	478
WS 986	1088	992	WS 1079	38	258
WS 987	475	577	WS 1078	175	230
WS 988	1825	1237	WS 1077	638	538
WS 989	1100	—	WS 1075	150	—
WS 996	875	1257	WS 1070	163	262
WS 997	1850	1413	WS 1069	375	370
WS 998	1900	1540	WS 1064	438	305
WS 999	2138	1778	WS 1063	500	—
WS 1000	2375	817			
WS 1001	7688	5145	WS 1056	83	162
WS 1002	4075	—	WS 1055	63	138
			WS 1054	275	503
			WS 1053	250	387
			WS 1052	200	447
			WS 1051	650	617
			WS 1050	2450	—

STABILITY OF THE WATER MASSES

To obtain some further comparison of the characteristics of the upper water layers on the two surveys the vertical stability of the water columns has been determined. This has been calculated approximately as $10^5 \, d\sigma t/dz$ for the layers 0–50 m. and 0–100 m., and is set out in Table 6.

In spite of the instability of the water at WS 976 the great stability of the upper 50 m. at all the other stations on survey I contrasts most vividly with the generally lower stability on survey II. This pronounced difference, the whole region being some ten times more stable in the upper 50 m. on the first than on the second survey, reflects clearly the difference in the meteorological conditions on the two surveys.

THE WATER MASSES

WATER MASSES OF THE SOUTH ATLANTIC

Wüst (1935) plotted T-S curves for three more or less meridional lines of 'Meteor' stations in the Atlantic Ocean. The remarkable similarity of these curves within the South Atlantic is at once apparent from his diagram (his p. 216). Excepting the upper layers where external factors come into play, the curves all fall within a regular pattern. A typical T-S curve for the South-east Atlantic is shown in Fig. 31.

The 'Bottom' water is a cold dense mass of water lying in the deeper basins. It originates in the Antarctic, where cooling processes in the proximity of the continent cause the water there to sink down the continental slope, and being very dense it spreads out across the ocean floor. The main centre of this sinking appears to be the Weddell Sea, but it probably also occurs at other points along the Antarctic coast. The water thus formed can be traced by its low temperature and salinity, and it describes a northward flow into the South Atlantic. Partly under the influence of the earth's rotation, but probably mainly owing to the bottom topography, the principal flow takes place up the western side of the South Atlantic. A certain amount of the water flows up into the Cape Basin, but this does not go far north since its passage is interrupted by the Walvis Ridge, a connecting ridge between the African continent and the Central Atlantic Ridge. Wüst (1935) demonstrated that the potential temperature of the bottom water south of the Walvis Ridge was about 1° C. lower than that to the north of the ridge where it was over 2° C. He suggests that the flow up the western side of the ocean infiltrates in a cyclonic movement through a gap in the Central Atlantic Ridge (the Romanche gap) and enters the Angola Basin from the north.

Lying above the bottom water, and extending up to nearly 1000 m. from the surface, there lies a great mass of water called the 'North Atlantic deep water'. Owing to its great homogeneity it occupies relatively little space on the T-S diagram (Fig. 31), the observations within it being clustered around an intermediate *maximum* of salinity. Taking other factors into account, however, Wust has shown that the deep water is, in actual fact, composed of three separate layers. As far as we are concerned the three deep water layers can all be taken together, and considered as having a general southward flow. The water leaving the North Atlantic does so principally on the western side, so that the best-defined flow in the South Atlantic is found down the South American coast, the movement in the eastern part of the ocean being much less well defined. On reaching higher latitudes the whole mass of deep water becomes directed to the east.

Above the deep water, there is a layer of minimum salinity. This characterizes the main axis of northward flow of the 'Antarctic intermediate water'. Formed by the sinking of antarctic surface-water, from the antarctic convergence in about 50° S., this layer moves northward at a depth of between 600 and 800 m. Again the strongest movement is on the western side of the ocean, and indeed

in the eastern South Atlantic there seems to be a tendency to an eastward movement, particularly in the Gulf of Guinea, where it apparently diverges cyclonically from the main northerly trend. Thus in the South-west African region the flow is again ill defined.

In the subtropical region between the surface-waters, and the salinity minimum of the antarctic intermediate water the T–S curves follow a nearly straight line relationship to within about 200 m. of the surface, above which the circulation becomes more complex within the tropical and sub-tropical surface and subsurface layers. This water mass, represented by the nearly straight line part of the curve, has been termed the 'South Atlantic central water' (Sverdrup, Johnson and Fleming, 1946). The process of its formation is still rather obscure. Sverdrup *et al.* (1946) suggest that it is probably formed by a simple process of sinking along surfaces of equal density in the region of the subtropical convergence, as the *vertical* T–S relationship of the South Atlantic
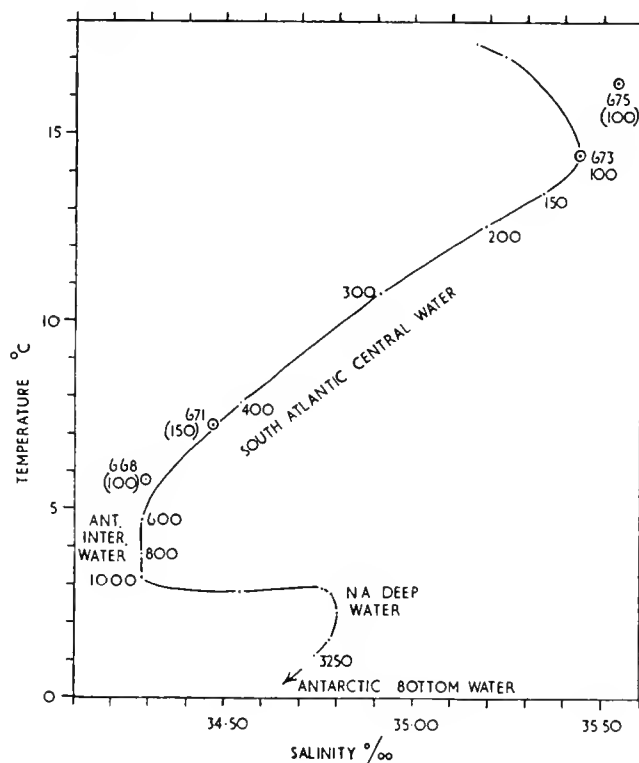
Fig. 31. A typical temperature–salinity curve for the south-east Atlantic, drawn from observations at 'Discovery' station 673. The water masses represented on the curve are named. The additional points in open circles are the T–S relationships at the stations (675, 671 and 668) at the depths (in brackets) shown. These stations lie in a north–south line across the subtropical convergence, so the points show the horizontal T–S relationships at subsurface depths across this region, indicating the close similarity to the vertical T–S curve for the South Atlantic central water. Depths are in metres.

central water corresponds closely with the *horizontal* T–S relationship in the subtropical convergence region (see Fig. 31). Clowes (1950), however, has taken exception to this view on the grounds that an examination of the surface T–S relationships in the region 0° to 20° E. and 30° to 40° S. fails to show any similarity to the vertical T–S curve of the South Atlantic central water. He considers that a more likely explanation is a direct mixing between the antarctic intermediate water and the sub-tropical surface- and subsurface waters, which would probably take place in the region of the sub-tropical convergence.

North of the antarctic convergence in about 50° S., where the antarctic surface-water sinks to form the intermediate water, there lies a belt of warmer water, the subantarctic water, whose characteristics suggest that it is a mixture of antarctic water and warmer water from the north. Extending north-

wards to the subtropical convergence, a distance of about 600 miles, this is a relatively shallow layer. Under a well-mixed surface-layer, which is rather poorly saline, there is a pronounced subsurface salinity maximum, and below this again the water becomes less saline.

It seems fairly certain (Deacon, 1936) that this subsurface salinity maximum represents the core of a southward flow within the subantarctic zone. The properties of this water suggest that it is replenished from two sources, from a subsurface highly saline current within the subtropical zone itself, and (to a lesser extent) from subantarctic water sinking at the subtropical convergence and returning to the south. The vertical T-S curve below the subtropical convergence suggests that the central water there is a mixture between water of higher salinity than the surface-water and the antarctic intermediate water (see Fig. 31), showing that it is probably the subsurface current which is involved in the mixture in this region. The subsurface salinity maximum is not generally distributed over the ocean, however, and no doubt elsewhere it is the surface-water which mixes with the inter-mediate water as occurs in the subtropical region itself.

Above the salinity maximum where present, and generally over the subtropical zone, the surface water is a fairly homogeneous layer, and its movements, governed principally by the trade winds, follow an anti-cyclonic pattern. From the Brazil current flowing southwards down the western side of the South Atlantic, the water is carried to the east with a decreasing southerly component. It appears to be the balanced effect of this movement with the northward drift of the subantarctic surface-water which is responsible for the maintenance of a sharp subtropical convergence. Deacon has already pointed out that there is not much likelihood of this water sinking at the subtropical convergence, and it is probably mostly carried east in a direction more or less parallel to the convergence. As it reaches the eastern side of the ocean, it turns more to the north, and, with perhaps a contribution from the Agulhas current (Dietrich, 1935a, b), it returns up the eastern side of the Atlantic as the South-east trade wind drift. Across the Atlantic, and forming a line approximately from Angola to Rio, about the 23° C. surface isotherm, there is a convergence of the surface-water, and to the north of this line there is a warm highly saline layer which is very poor in nutrients and sharply divided from the under-lying water by a strong discontinuity layer. This is the tropical surface-water, which owes its existence to the immense amount of heating and evaporation in this region. From the African side the south equatorial current carries this water across the Atlantic to Brazil, somewhat in the form of a left-hand screw. Within itself the layer is homogeneous and well mixed.

TEMPERATURE-SALINITY RELATIONSHIPS OF THE SOUTH-WEST AFRICAN WATERS

The typical T-S curve for the offshore stations of the 'William Scoresby' is very similar to the general pattern described for the South Atlantic.

None of the 'William Scoresby' stations was in deep enough waters to encounter the Antarctic bottom water which the 'Meteor' observations showed to fill the depths of the Cape Basin, but at all stations of sufficient depth off the continental slope the North Atlantic deep water was encountered. At WS 976 only, a maximum salinity of 34·91 ‰ at 2420 m. was recorded. This represented the nearest observation to the core of the upper deep water, but at all other stations salinity values around 34·80‰, and still increasing at the lowest depths of observation, indicated that the central core of the upper deep water had not been reached.

Sometimes between the southward flow of the North Atlantic deep water and the northward flow of antarctic intermediate water, a slight temperature inversion is produced, such as was recorded at station WS 996 where the water at 1470 m. with a temperature of 3·05° C. was 0·04° C. warmer than the water at 1170 m. Deacon has recognized this layer of minimum temperature, but considers that

the flow of the intermediate current is principally in the layer of minimum salinity, and that its flow in the layer of minimum temperature is probably much affected by turbulent mixing with the underlying deep water.

A well-marked layer of minimum salinity was encountered at all stations off the continental shelf on both of the surveys. Table 7 shows the depths and observed salinities in the layer of minimum salinity. Wüst developed a method for studying the mixing path of a water type from its T-S relationships. Initially the water type is plotted as a point on a T-S diagram. As it mixes with adjacent layers
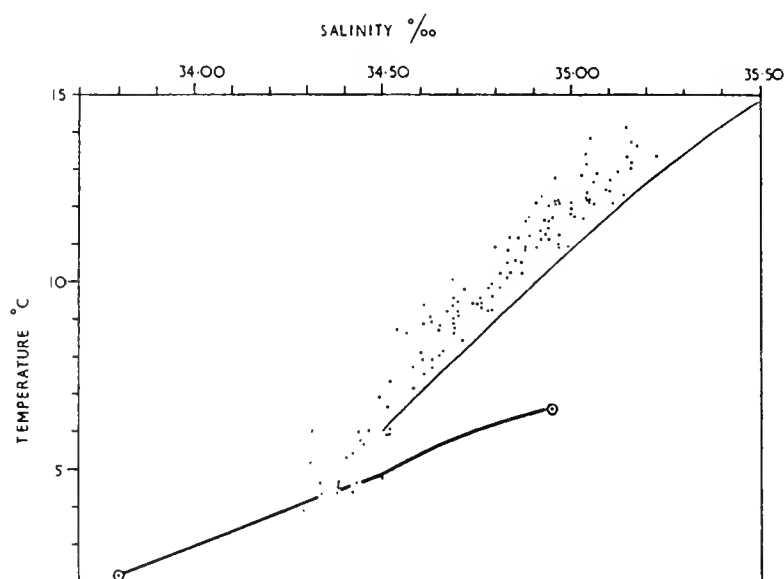
Fig. 32. Temperature–salinity relationships of the water layers between 100 m. and the salinity minimum of the Antarctic intermediate water. The heavy line shows the relationship in the core of the Antarctic intermediate water from its source (left) to its northern limit (right), after Wüst, 1935. The thin line is the line characteristic of South Atlantic central water (Sverdrup, 1946).

the point moves along a line, until eventually its characteristic, say a salinity minimum, disappears (Fig. 32). Thus one can follow the water type from its beginning until it is completely obliterated by mixing with other waters. This method is known as the 'Kernschichte methode'—the core method. Applying it to the intermediate water one finds that in the core of the antarctic intermediate layer the effect of vertical mixing has altered the T-S relationship from the original water type (T = 2·2° C., S = 33·80‰) to a value of T = 4·7° C., S = 34·4‰ off South-west Africa (Fig. 32). As the salinity

Table 7. *Salinity minima in the antarctic intermediate layer*

Station	Salinity minimum (‰)	Depth (m.)
WS 976	34·50	700
WS 977	34·34	820
WS 978	34·45	600
WS 986	34·38	800
WS 996	34·34	600
WS 997	34·31	570
WS 1056	34·33	600
WS 1070	34·42	600, 820
WS 1080	34·38	780
WS 1081	34·29	990
WS 1102	34·31	630

The figures show the minimum values of salinity recorded at 'William Scoresby' stations, and the depths of the observations.

minimum finally disappears at T = 6·6° C., S = 34·95‰ in about 15° N., so we can consider that the antarctic intermediate layer off South-west Africa contains only about 50% of the original water type.

Above the antarctic intermediate water core, and to within 100 m. of the surface, all the 'William Scoresby' observations fall fairly close to a nearly straight line joining the points T = 14·0° C., S = 35·20‰ and T = 4·7° C., S = 34·40‰. It will be seen that this line lies somewhat to the left of Sverdrup's curve for the South Atlantic central water (Fig. 32) (Sverdrup et al. 1946), but it should be remembered that Sverdrup has taken a mean curve for the whole South Atlantic.

Above 100 m. external influences come into play and the water becomes subjected to heating, cooling, evaporation, etc., and these account for the more widely spaced distribution of the T-S points. But the effect of these external influences is fairly well defined and with caution it is possible to derive at least some information concerning the surface water-layers from their T-S relationships.

WATER MASSES OF THE UPPER LAYERS (0–200 m.)

Oceanic and coastal surface-waters

The different types of surface-water which were recognized from the general distribution of temperature and salinity (p. 174), form, of course, a natural grouping for the T-S curves of the upper water masses. As the upwelled water has been brought to the surface from some subsurface depth offshore, its T-S characteristics are similar to those of the water at the depth from which it was upwelled, except that it has undergone a certain amount of modification in the process of uplift.

If we compare an inshore and offshore station on the first survey—stations WS 1000 and 996 (Fig. 33a)—it is clear that at the inshore station the upper 50 m. is composed of a mass of water corresponding to that at 200 m. at the offshore station, but warmed up, reaching a temperature of 18° C. at the surface. The low salinity (34·9‰) of this water on the surface contrasts strongly with the high salinity (35·18‰) of the oceanic surface-water. Similarly on survey II (in Fig. 33b) there is again a contrast, although rather less pronounced.

The T-S diagrams also demonstrate clearly the mixed nature of the water inshore at Walvis Bay on survey I. Comparing Fig. 33c with Fig. 33a, we can see that the surface-water at stations WS 979 and 980 lie somewhere between the true oceanic and true coastal characteristics.

Finally, for the 25° S. line on the first survey the T-S diagrams (Fig. 33d) show the 'oceanic' characteristics of the inshore 'station'.

We see, therefore, that the upwelled water originates from the South Atlantic central water, at depths of 200–300 m. Apparently the upwelled water is not subjected to any significant mixing with the warmer and more saline 'offshore' surface-waters in its process of uplift. Indeed, everything suggests that it remains quite discrete from the latter. On the sea surface, as we have already seen, there is in most cases a sharp boundary between the two types of water except in areas where mixing has obviously taken place.

It is evident that these two water masses form, on both surveys, a series of eddies along the coast, tongues of upwelled water diverging offshore and inter-locking with wedges of offshore water converging towards the coast. It is difficult to generalize about the depth to which the eddies extend, as some of them appear to retain their identity to the depth of upwelling while others are very much shallower.

Dynamic height anomalies

Owing to the lack of direct observations of surface-currents it has been necessary to resort to some indirect method of estimating the actual water movements which were taking place during the surveys. The most widely used of such methods is that based upon the theorem developed by Bjerknes

(Sandstrøm, 1919). Other methods, such as the isentropic analysis used by Montgomery (1938), have in certain cases an advantage, but after experimentation with both methods, and bearing in mind that the observations do not properly satisfy the requirements of either, a straightforward presentation of the dynamic height anomalies has been made. A few words may be said about the theoretical implications of this method in so far as the present work is concerned.
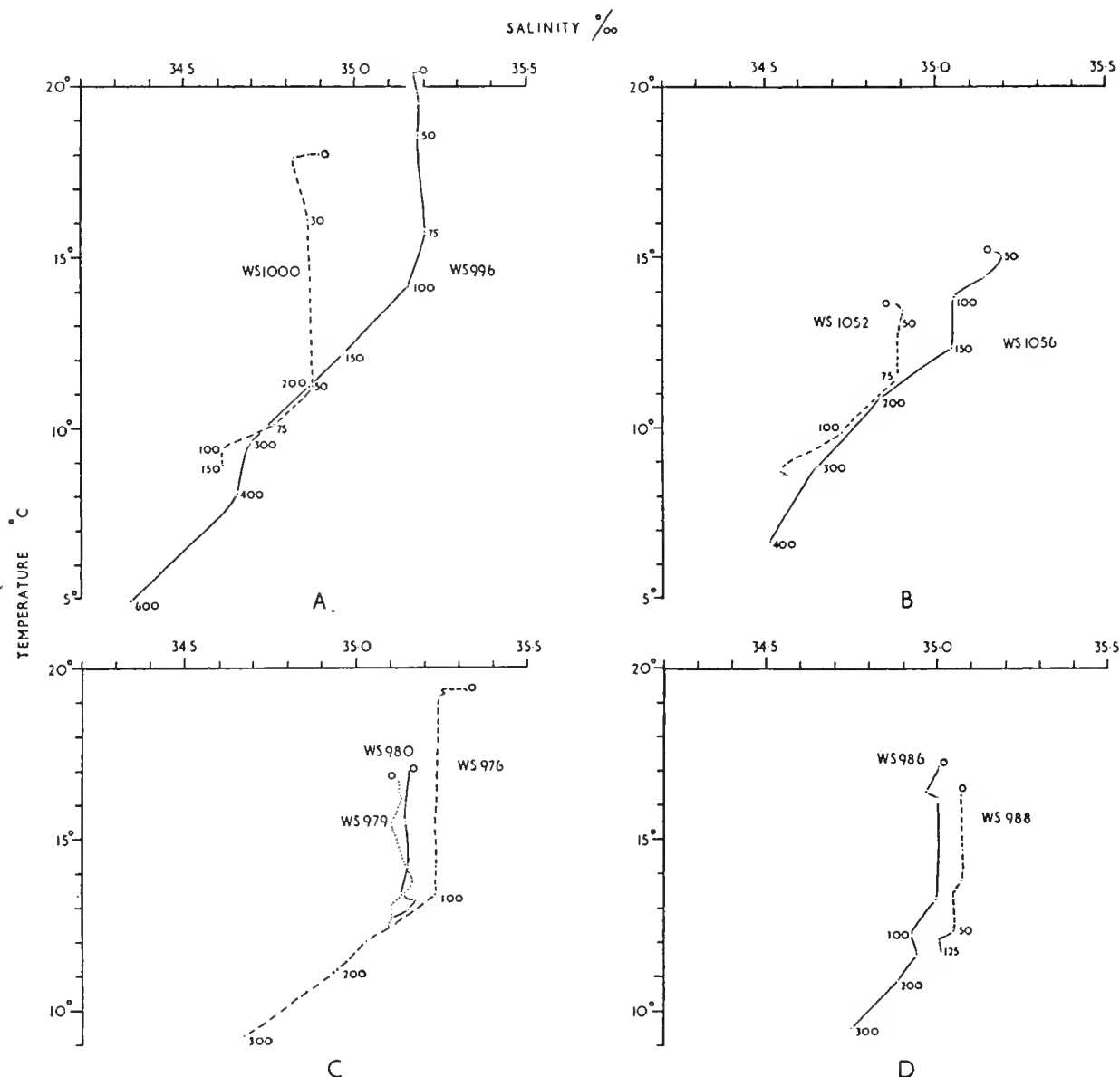
Fig. 33. Temperature–salinity relationships at 'William Scoresby' stations. (a) WS 996 and WS 1000 (broken line) off Orange river mouth, survey I. (b) WS 1052 (broken line) and WS 1056 off Orange river mouth, survey II. (c) WS 976 (broken line), WS 979 (dotted line) and WS 980 off Walvis Bay, survey I. (d) WS 986 and WS 988 (broken line) off Sylvia Hill, survey I. Positions of stations are shown in Figs. 1 and 2.

First it should be noted that Bjerknes's theorem applies to currents in which a state of 'stationary motion' is maintained. In other words, it assumes that while the current flows the distribution of mass in the water remains unaltered. This implies that no mixing, or change in properties of the water particles along their path, may take place, and that no vertical translatory movement should occur. On these assumptions the horizontal movement of the water can be related to the distribution

of mass within that water. Parr (1938 *b*) has already emphasized the importance of these points in interpreting charts of dynamic height anomalies.

In the waters off South-west Africa, it is quite obvious that the requirements of Bjerknes theorem are not satisfied. Clearly the wind in this region has a considerable effect on the sea-surface, and there are undoubtedly considerable vertical movements of the water masses. It is therefore considered unwise to place too much reliance on the charts as depicting actual currents, but rather to look upon them as plans of the distribution of mass within the water above an arbitrary level surface.

In the construction of the charts it is desirable to choose a surface of no motion, above which the mass of water can be calculated. In the present observations it is impossible to be certain that such a surface does exist. Normally such a surface is chosen at a considerable depth, where the movements, if any, will be so small relative to those at the surface that they can be ignored. The 'William Scoresby's' observations lie, however, for the greater part in shallow waters, and there is little likelihood that any level will present a surface of no motion in these observations[1]. As the best compromise, however, the 600 decibar surface has been chosen, and the topographies of the sea-surface, and the 200 db. surface, are shown relative to this in the charts in Fig. 34. Many of the present observations have been made in the relatively shallow waters of the continental shelf where they cannot extend to the depth of the reference surface chosen in the deeper water offshore. Helland-Hansen (1918) proposed a method to overcome this difficulty. He suggested that the land mass in the vertical section representing the continental shelf and slope, should be replaced by a fictitious body of water which is considered to be at rest, and in which the isosteric surfaces would, therefore, be horizontal. In the adjacent water mass the isosteric surfaces would tend to become horizontal as they approach the continental slope, for, owing to friction, the velocity along the sea-bed must approach to zero. For this reason Helland-Hansen suggested that the isosteres as they approach the sea-bed should be drawn horizontal and produced horizontally through the land mass, thus furnishing arbitrary levels for the calculation of the heights of the isobaric surfaces over the land mass. In face of the difficulties this seems a fairly reasonable assumption to make, but it has no physical basis whatsoever, and it is indeed difficult to imagine the existence of such an arrangement. Groen (1948) has discussed another method which was suggested by Sverdrup, and proposed yet another, that of continuing the isosteric slopes into the land mass, but it is doubtful whether these produce a picture any more realistic than that given by Helland-Hansen's method which has been used in the following.

Although a precise picture of the currents at different levels cannot be attained, it is intended that the charts should at least serve as a check on the water-movements deduced from the distribution of temperature, salinity and other properties of the water masses. The movements shown will probably be more correct during survey I when there was less vertical movement, than during survey II.

Surface topography (Fig. 34)

On survey I the most pronounced feature of the chart shows the tendency to a movement towards the coast in the latitude of Walvis Bay (23° S.). This flow appears to bend southwards along the coast and is no doubt responsible for the mixed nature of the water inshore at Walvis Bay, and the pronounced oceanic influence at the inshore stations on the 25° S. line. In its southerly movement, it displaces away from the coast the north-westerly flow of coastal waters from the south, so that in 25° S. there is a southerly movement of mixed oceanic water inshore, and a northerly movement of coastal water offshore.

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[1] Attempts to define a level of no motion using techniques such as that of Sverdrup and Flemming (1941) have given little guidance with the present observations beyond suggesting that the 600 decibar surface may be one of relatively little motion.
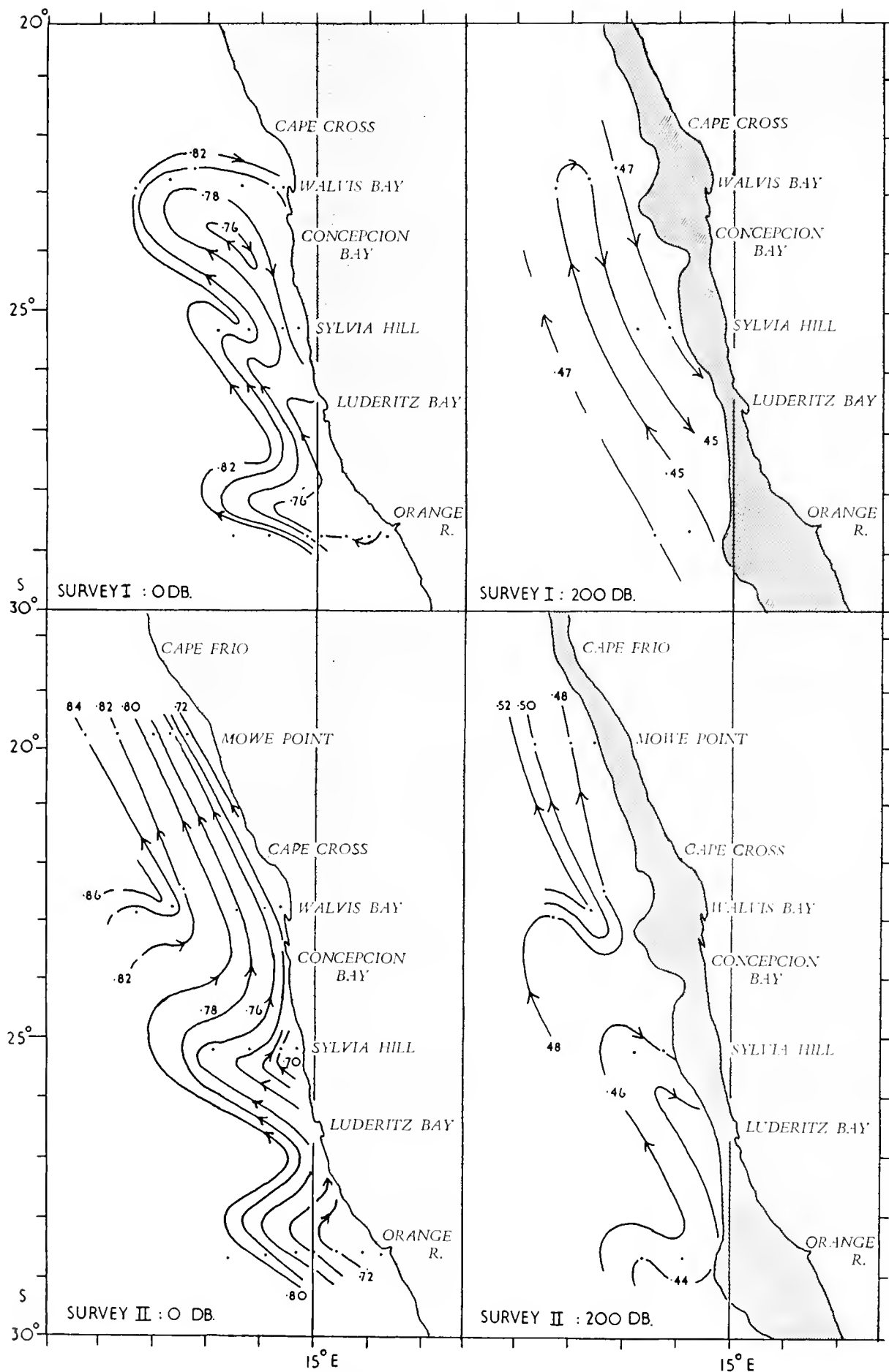
Fig. 34. Dynamic height anomalies of the sea-surface and 200 db. surfaces relative to the 600 db.
surface, for survey I and survey II.

The eddy which lies to the north of the Orange river line is probably a fair representation of the westerly flow of coastal water adduced from the temperature and salinity observations.

On survey II the movements are considerably more intense. Undoubtedly the sparsity of data shows a simpler picture than is shown in the surface-temperature chart (Fig. 7b) which is constructed from a much greater number of observations, but within the three great eddies shown, the cooler coastal waters show a pronounced offshore, or longshore movement to the north and west. In conjunction with this the oceanic waters move in an easterly direction towards the coast.

There were very few occasions on which the set of the ship could confidently be ascribed to water-movement as distinct from wind leeway. At the station on the outer end of the Walvis Bay line on survey I a northerly set of about 1 knot was encountered with a light wind. This agrees with the computed currents (Fig. 34). The only other occasion upon which we can be reasonably certain the effect was solely due to currents was between stations WS 1057 and 1061 on survey II. When the ship was steaming north from the Orange river line stations to the inshore end of the 25° S. line, she was set 065° at ½ knot with no wind. Once more this is in agreement with the computed currents.

Topography of the 200 db. surface

The lesser number of observations at this depth give the appearance of a very simplified pattern. On survey I there is clearly a southerly movement along the coast from the north, penetrating southward and tapering in towards the coast, and finally disappearing in about 28° S. Seawards of this the water appears to move to the N.N.W.

On survey II offshore the principal movement is once more to the north, but there is some indication of a south-easterly flow on the landward side of a trough line running north-west through WS 1070. This tendency to a southerly or onshore movement at this depth in the water adjacent to the continental shelf will later (p 190.) be seen to be connected with the process of upwelling. It is postulated that this is a compensatory movement replacing the water which has been drawn up to the surface inshore and we have, therefore, called it the compensation current.[1] This southerly current is warmer and more saline than the waters seaward of it in the trough which separates it from the northerly current farther offshore.

THE WATER MASSES AT 200–600 m.

Generally speaking, on both surveys, the waters in this layer correspond very closely with the mean temperature-salinity relationship already outlined for the South Atlantic central water. Table 8 gives the salinity values corresponding to the given temperatures at each station. On the first survey the mean range of salinity at the given temperature is only 0·11 ‰, and on the second survey 0·10 ‰.

Table 8. *Temperature–salinity relationships of the water masses between 200 and 600 m.*

Tem-perature (° C.)	Survey I WS 976	WS 977	WS 978	WS 986	WS 996	WS 997	Survey II WS 1102	WS 1100	WS 1098	WS 1080	WS 1081	WS 1079	WS 1070	WS 1056	WS 1055
12·0	—	—	—	—	—	—	35·03	35·10	35·10	—	—	—	—	—	—
11·0	34·91	—	—	—	34·83	34·82	34·91	34·97	35·00	34·87	34·90	34·90	—	—	—
10·0	34·76	34·84	34·73	34·79	34·73	34·72	34·80	34·84	—	34·74	34·81	34·82	34·80	34·76	34·78
9·0	34·65	34·75	34·67	34·70	34·67	34·63	34·72	34·72	—	34·66	34·71	34·75	34·69	34·67	34·68
8·0	34·56	34·65	34·61	34·60	34·64	34·62	34·60	34·63	—	34·59	34·63	34·67	34·65	34·59	34·59
7·0	34·52	34·58	34·55	34·52	34·55	34·57	34·44	34·56	—	34·51	34·54	—	34·57	34·52	34·50
6·0	34·52	34·52	34·48	34·45	34·44	34·44	34·31	34·51	—	34·43	34·66	—	34·47	34·45	34·43
5·0	34·51	—	—	—	34·34	34·31	—	—	—	—	—	—	—	34·36	34·39

The salinity values, corresponding to the given temperatures at each station are shown in parts per thousand. Mean: Survey I = 0·11 ‰; II = 0·10 ‰.

[1] Yoshida and Mao (1957), and later workers have shown that divergence and consequent upwelling at the surface is likely to be accompanied by a poleward movement in the subsurface layer.

It may be said, therefore, that on the basis of the temperature–salinity relationship, it is not practicable to distinguish any significantly distinct water masses in the layer 200–600 m., and also that it is all characteristic of the South Atlantic central water. As will be shown later, however, when dealing with the non-conservative properties oxygen and phosphate, a very marked distinction is present in this layer.

THE ANTARCTIC INTERMEDIATE WATER

The depth distribution of the observed salinity minimum in this layer has already been given in Table 7. It is noteworthy that at its core off South-west Africa only 50% of the original water type is present. Later it will be shown that the upwelling takes place from considerably lesser depths than this, and it is in fact South Atlantic central water which is upwelled and not, as has often been supposed, the Antarctic intermediate water. It is true that the former may contain a little of the latter but the proportion of antarctic intermediate water must be extremely low.

UPWELLING

PREVIOUS WORK ON THE MECHANISM OF UPWELLING

Several explanations have been put forward to account for the presence of the cold water along the south-west African coast. The earliest idea held was that the Benguela current was a continuation of the west wind drift, bringing down cold water from the higher latitudes of the antarctic. Ross (1847) (see p. 132), however, demonstrated that this could not be true because warmer water was present to the south of the Benguela current, cutting off any continuous flow from the antarctic. Yet this view was maintained by some authorities even as late as 1910 (Engeler). Ross did not offer any satisfactory alternative explanation to the South Polar current theory, but later workers gradually developed the idea that the cold water must come up from subsurface layers. Several suggestions were made as to how this uplift, or upwelling, came about. Witte (1880) deduced on theoretical considerations that the upwelling must be brought about either by the effect of the earth's rotation on such a meridional current as this, or possibly by offshore winds driving surface-water away from the coast. Murray (1888, 1891) showed the latter to occur in the lochs on the west coast of Scotland, where, in summer-time, offshore winds produced a depression of the surface temperature along the shore. Buchanan (1880) and Buchan (1895) held that the same process was of general application to the major upwelling regions off the west coasts of the continents. Schott (1902), however, while considering that the upwelling along the north-west African coast could be explained on these grounds (as the winds blow either parallel to the coast or offshore), pointed out that this could not hold good for the south-west African coast. Here the winds were principally onshore in the coastal region.

Schott offered an alternative explanation. Since the main impulsive force of the Benguela current was the south-east trade wind, the current would be deflected, under the influence of the earth's rotation, away from the coast. The water thus removed must be replaced, and owing to the direction of the coastline this would have to be a vertical compensation. This theory Schott supported with the fact that where the African coast recedes to the north-east (in about 17° S.) the upwelling fades out and becomes an irregular phenomenon, the compensation flow then being able to take place horizontally on the sea surface from the north-east.

Thorade (1909) states, with regard to the California current, that 'Auch dieser Grund kann für uns nicht in Betracht kommen, denn einmal ist unser Auftriebgebiet bedeutend weiter von Äquatorialstrom entfernt, und dann entwickelt sich dieser [the trades] am Kräftigsten gerade während der Wintermonate, in denen die Auftrieberscheinung im Rückgange begriffen ist'. Thorade proceeded

to explain the Californian upwelling by Eckman's theory of currents. He showed that the upwelling is a direct effect of the coastal winds which on the assumptions of Eckman's theory need not blow offshore to produce an offshore transport of surface water. A wind blowing parallel to the coast would be sufficient to induce such a transport with consequent upwelling.

Sverdrup (1938), from a detailed examination of the Californian current, supports this view, and concludes that the upwelling is a direct effect of the local winds transporting surface-water away from the coast. Gunther (1936) found that on the Peru Coast the 'William Scoresby's' observations indicated that the upwelling was brought about 'as a result of wind acting in conjunction with forces due to the earth's rotation'.

The present work indicates that while the trade wind in the open ocean must maintain the denser water nearer the surface inshore, the periodic and local intense upwelling is probably mainly dependent upon the local coastal winds producing a northwards, longshore or offshore displacement of the surface water, thus initiating a vertical compensation flow from the subsurface layers.

Ekman's theory (1905) provided the basis of our present-day understanding of the effect of wind stress on the sea-surface. It shows us qualitatively that, owing to the effect of the earth's rotation and frictional forces, the drift produced by a wind blowing over the ocean deviates at an angle of $45°$ to the left of the wind direction in the southern hemisphere. Owing to the viscosity of the water, the velocity in this drift current will decrease regularly with depth. There will also be an increased deflection with depth, until a point is reached where the current is directed against the surface drift. At this point the velocity of the current is about 1/23rd of that at the surface, and Ekman has termed this depth (D) the 'depth of frictional influence'. While the current vectors at different levels in the wind current vary, the total transport remains directed normal to the wind direction (that is $90°$ to the left in the southern hemisphere).

These results apply to an ocean of which the bottom is very deep, and where the influence of coastline and varying density of the water is not considered. In this latter respect, the quantitative application of the theory is hindered, as the magnitude of the reaction between the different density layers in the sea is not known. Eddy viscosity is, however, a measure of this reaction, and more recently Rosby and Montgomery (1935) have introduced the conception of a 'mixing length' which varies with depth and upon which the eddy viscosity is dependent. On this basis they find that the deviation of the drift is not constant as Ekman postulated, but varies with the strength of wind and with the latitude. Even these improved assumptions, however, still appear to fall short of giving a realistic picture.

Ekman further studied the problem of wind drift in the presence of coastlines and where the sea bottom was shallow. Where the bottom is greater than twice the depth of frictional influence it does not have much influence, but in shallower water there is a restriction of the deflection and slowing of the turning with depth, until in very shallow water the whole movement follows the direction of the wind (the effect of the earth's rotation in this case being negligible). Thus in coastal regions three main factors affect the wind drift.

1. The position of the coastline in relation to the water in question.
2. The relation between the depth D and the sea bottom.
3. The direction of the wind stress, in relation to the direction of the coastline.

The effect of winds on the South-west African coast

We can find the approximate magnitude of D in metres from the relationship:

$$D = 7\cdot6\ W/\sqrt{\sin\theta},$$

where the wind stress W is expressed in m./sec., and θ is the latitude. (For wind stresses <6 m./sec.

the formula is replaced by $D = 3 \cdot 67 \sqrt{w^3}/\sqrt{\sin \theta}$ (Sverdrup *et al.* 1946).) Even with force 8 winds the depth D is of the order of 200–250 m., and therefore it is evident that only in the coastal region will D have an effect upon the wind current. The region where the south-east trade prevails, outside the continental shelf, will be void of any bottom-effects.

Thus in the open ocean the south-east trade wind will produce a surface drift in a westerly direction and a total transport of water to the south-west. The lighter surface-water will therefore be transported away from the African coastal region. The presence of the coastline, however, prevents any surface replacement of this water in the coastal region, and therefore a vertical replacement or upwelling must follow. This vertical movement in the coastal region will create a distribution of density such that the heavier water lies against the coast, and a relative current will be produced running northward along the coast.

The intensity of this relative current will depend upon both the direction of wind and the direction of the coastline. Now, in South-west Africa, the coast runs N.N.W. to S.S.E. and the trade wind is south-easterly becoming more southerly in higher latitudes. The angle between the wind and the coast increases, therefore, from south to north, and one might expect from this an intensification of the relative current to the north.

The total transport of the wind current is, however, directly proportional to the wind stress and inversely proportional to the sine of the latitude, so the decreasing strength of the trade wind to the north of the region will tend to reduce the intensity of the relative current. The ultimate development of the latter will depend on the magnitude of these various effects.

The winds in the coastal region must have an additional modifying influence on the relative current set up by the trade wind. Furthermore, as we pass into the coastal region the sea bottom, rising to the continental shelf, will have an increasing effect on the deflection of the wind current from the wind stress. It is not practical, however, to calculate the deflection as the coast is approached, since the wind also veers the nearer the coast one gets.

OBSERVED WINDS AND HYDROGRAPHICAL CONDITIONS

The synoptic charts of the South-west African Weather Bureau show that in September–October the trade winds were consistently stronger than in February–March. Theoretically this would have given rise to a greater relative current along the coast in the former months.

To estimate the effect of the coastal winds upon this relative current the wind vectors for three coastal stations have been plotted (Fig. 35) on the assumption that they would produce a surface drift at 45° to the left of the wind direction. All such vectors producing a drift between a line parallel to the coast to the north and a line normal to this offshore, have been considered positive, while all other winds have been taken as negative. From this figure it can be seen that during the first survey the coastal winds would only be expected to intensify the relative current off Luderitz Bay, little effect being exercised by the light winds and calms at Walvis Bay and Orange river. On the second survey in September–October there was a greater amount of coastal wind, particularly at Walvis Bay and Luderitz Bay. At Luderitz, it was predominantly positive and so would have intensified the relative current, while at Walvis Bay the greater variation of direction might have been contributory to a more rapid breakdown of the relative current into eddies.

The relatively calm spells at Walvis Bay and Orange river in March are reflected in the absence of convection layers in these sections while the greater wind stress in spring is associated with better mixed inshore waters in that season (Table 5).

A comparison of these features of the wind activity with the distribution of surface temperature and salinity on the two surveys suggests that the localized intensification of upwelling and indeed the

breakdown of the relative current into eddies may be largely dependent on the localized coastal winds. Clearly, however, a correlation between such observations as wind observed at coastal stations, within some modifying influence of the land, and hydrographical observations at sea must at best be rather rough, and a more satisfactory correlation might be expected if it were possible to compare the winds at sea with the coincident hydrographical changes. The only opportunity which we have of making
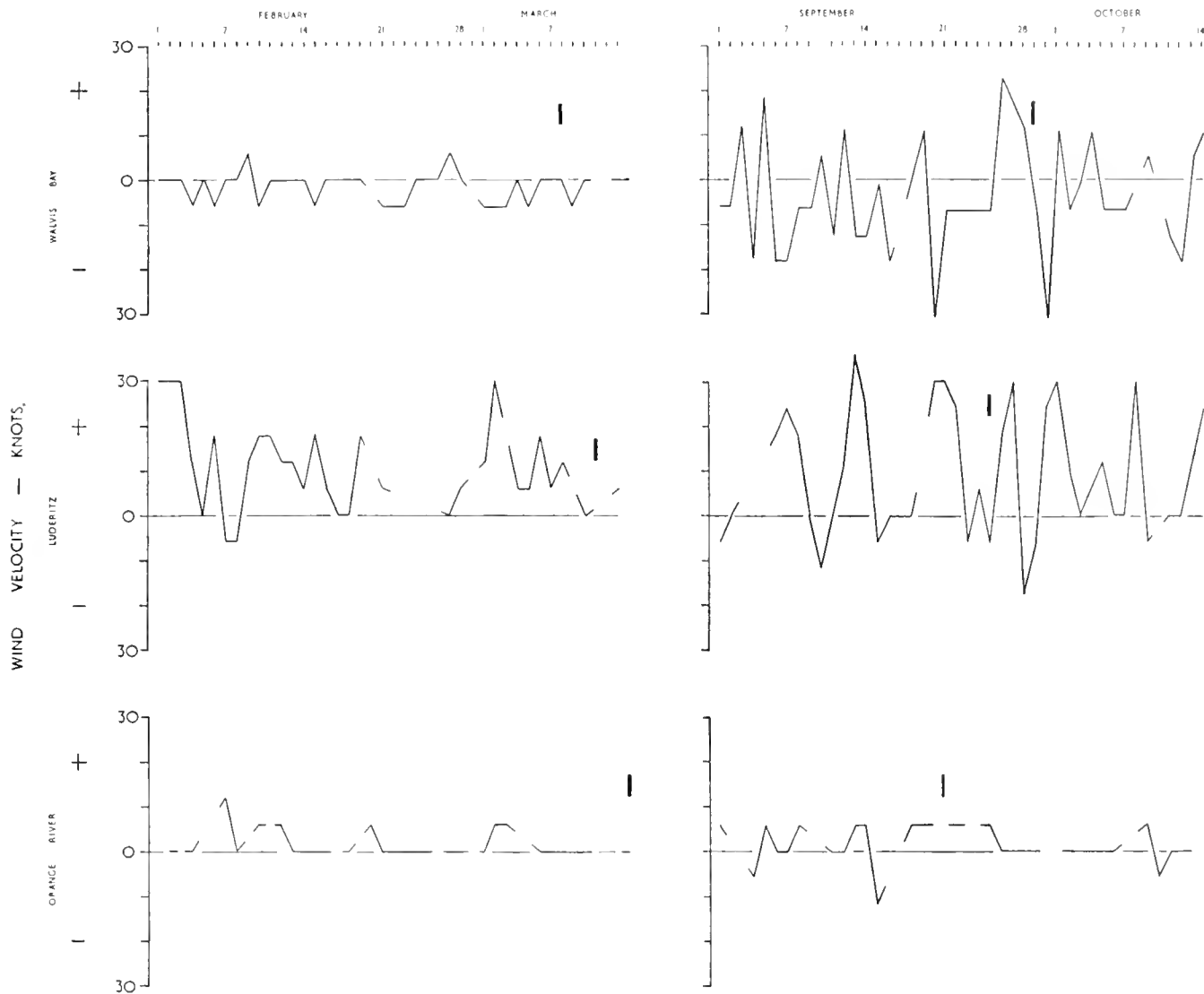
Fig. 35. Predominant coastal wind vectors before and during the two 'William Scoresby' surveys at three points on the coast—Walvis Bay, Luderitz Bay and Orange river mouth. Winds which would produce a longshore northwards, or off-shore drag on the sea-surface are taken as positive and other winds as negative. Wind speeds are in knots. Heavy black lines indicate the beginning of the survey in each position.

such an estimate of the short-term effect of the wind on the sea-surface was the occasion of a S.S.E. gale off Walvis Bay. While steaming west along the Walvis Bay line on the second survey the ship was forced to heave-to for nearly 48 hr. When the gale subsided the ship returned eastwards, and a comparison of the sea-surface temperatures before and after the gale reveals some interesting features.

In Fig. 36 the sea-surface isotherms have been drawn from the station observations and the distant-reading thermograph records; they are in black for the westward passage preceding the gale, and in red for the eastward passage following the gale.

During the period of this gale the wind records at Walvis Bay do not show any particularly stormy trend, and so it appears, as indeed one might expect, that the gale was solely due to increased velocity of the trade wind.

In interpreting the results certain assumptions must be made. First, surface heating must be assumed to have been regular within the region in question. Secondly, the turbulent mixing of the upper water layers must be assumed not to have had any great effect in the lowering of temperature in the surface waters. This latter seems justifiable since the depth of the mixed layer at WS 1079 before the gale was 50 m., and within this the temperature was nearly uniform.
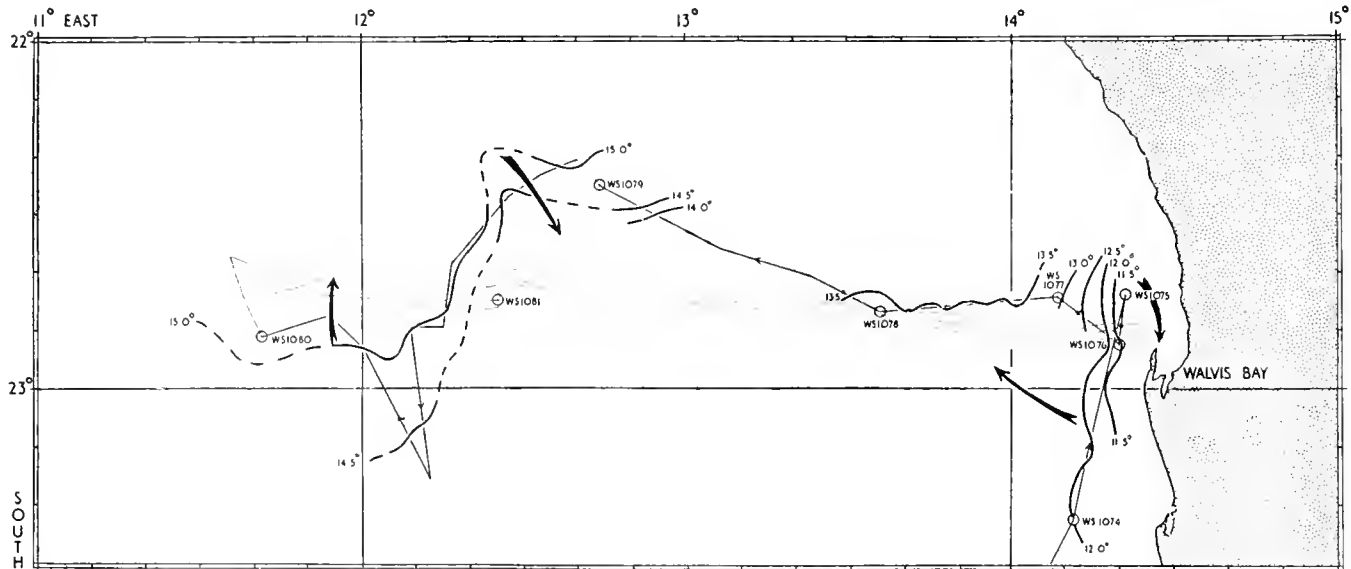
Fig. 36. Effect of wind and surface-temperature. The ship's track, stations and isotherms are shown in black for the westward passage along the line of stations off Walvis Bay. While at the seaward end of this line, a S.S.E. gale was encountered which blew for about 24 hr. at Beaufort force 8–9. Subsequently the ship returned eastward to Walvis Bay, completing WS 1081 en route, and the track and isotherms on the return journey are shown in red. Probable surface water-movements during the interval are indicated by the arrows.

If these assumptions are correct we can imagine that the clockwise rotation of the isotherms offshore was indeed the result of a clockwise water-movement. The change inshore suggests that an offshore movement south of the line had been accompanied by a landward compensation flow in two wedges, one moving south through the position of WS 1081, and the second right inshore at Walvis Bay.

THE MECHANISM OF UPWELLING

With the accumulation of further theoretical knowledge of the movements of ocean currents it was soon to be realized that upwelling was probably a far more complex process than a simple uniform uplift of the subsurface layers. Without any factual data at his disposal, Bobzin (1922), in the third part of his work, viewed the movements of the Benguela current from a theoretical angle. His deductions, based on a consideration of the general principles of the movements of ocean currents, suggested that the Benguela current existed in the form of a left-handed screw, proceeding towards the equator. This conclusion, in view of later work, seems to have been almost a premonition.

Gunther (1936) found from the 'William Scoresby' observations in the Peru current that the upwelling was a localized phenomenon, and took place within a series of well-defined horizontal eddies, while Defant (1936) working on the 'Meteor' data from the South-west African region developed

a schematic system for the upwelling there, although his data were too widely scattered to obtain as detailed a horizontal picture as Gunther did.

Defant started by considering theoretically what events would occur in a long straight canal over which a wind was blowing. If two bodies of water of different density are superimposed in the canal, and if the canal runs north and south in the southern hemisphere and has a wind blowing over it from
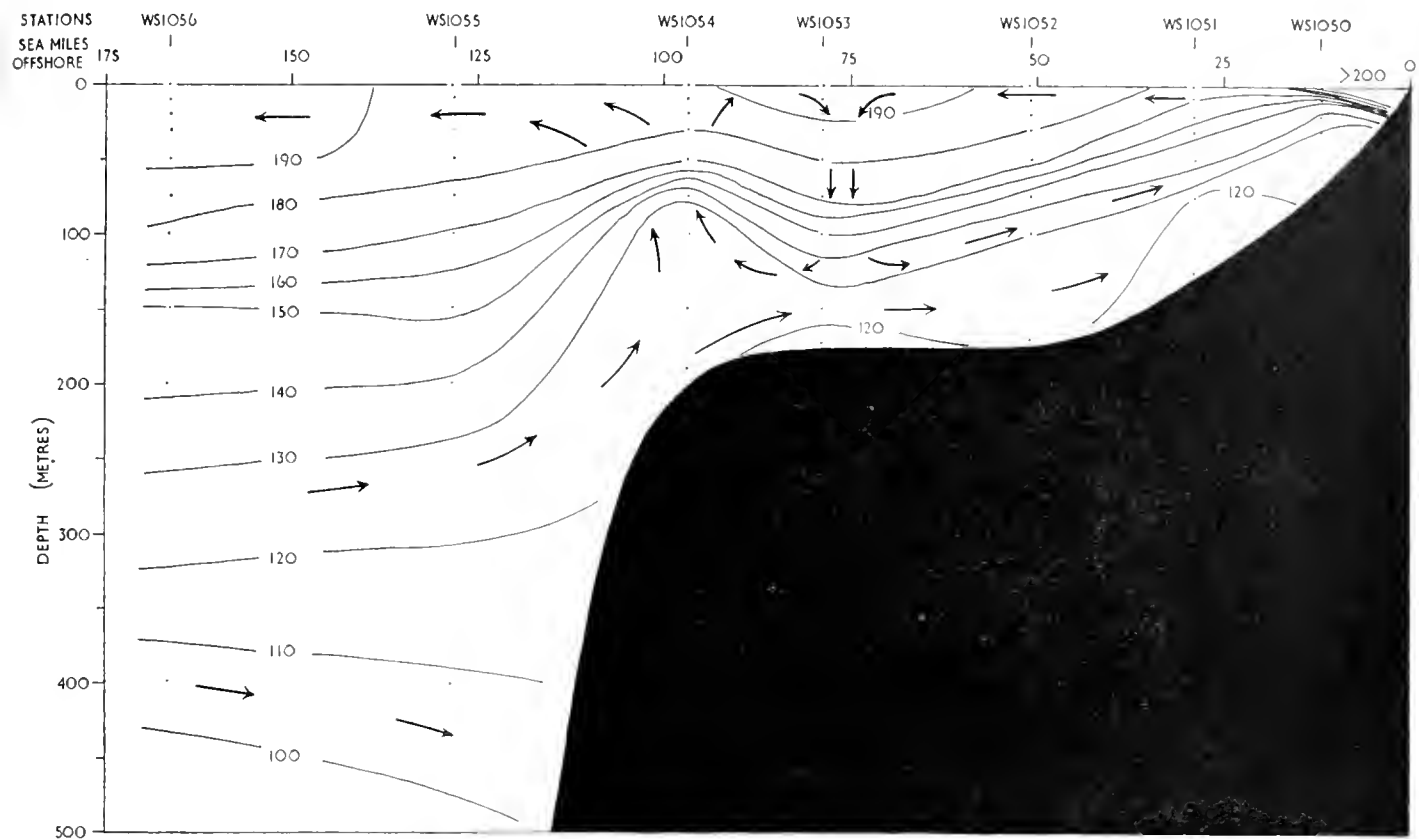
Fig. 37. Distribution of the anomaly of specific volume. Section off the mouth of Orange river on survey II. The probable direction of water-movement in a vertical plane, deduced from the shape of the isosteres, is also indicated. Positions of stations are shown in Fig. 2.

south to north, then the upper water layer would be set in motion. Under the provisions of Ekman's theory of wind drift, and when the thickness of the upper water layer is greater than the depth of frictional resistance, the lower water layer should remain at rest, while the boundary between the two would take up a slope across the canal. This slope would rise to the right (east, if one faces in the direction of flow of the surface-current) and thus the underlying heavier water would accumulate on the right-hand side of the current. At the same time a transverse circulation would form in the upper layer, which would depend on the velocity and direction of the wind. The upper layer circulation will form a left-handed screw motion. This would be strongest if the wind blew from the east, and suppressed if it blew from the west.

Applying these deductions to the South-west African coast we can regard the coast as the canal bank on the east. The west bank is missing, but this does not matter since the wind which is being applied (the south-east trade) is of limited lateral extent. Defant thus deduced a circulation pattern as in his fig. 7. The circulation is complicated by the fact that in the sea there are not two separate well-defined density layers but a general increase of density with depth. The trade wind induces a transverse circulation similar to that in the canal, a horizontal axis being present above which the water

9-2

moves to the west, while below the water rises to the east. The trade wind, however, does not extend right into the coast, and so inside its coastal boundary the surface-water is not drifted to the west, but moves north purely by virtue of the distribution of density. This agrees with the conception of a one-sided divergence which Defant derived from the surface-current pattern and showed in his fig. 7.

Sverdrup (1938) was more fortunate than Defant in having at his disposal detailed repeated observations off the coast of California. From these he was able to calculate directly a vertical velocity-profile across the upwelling region, and to relate it to the prevailing wind vectors as recorded at coastal stations during the surveys. From this, Sverdrup argues that as upwelling occurs along the coast, the dense upwelled water is in time transported offshore as was the surface-water which it arose to replace. Eventually conditions will be set up whereby a convection cell develops between the denser water lying on the surface and the lighter offshore water, this cell becoming sharply enough defined to be regarded as a boundary.

That such a mechanism operates on the South-west African coast we cannot be certain, but the available evidence strongly suggests that it does. The pattern of the isosteres on the Orange river line (survey II, Fig. 37), which is probably the most complete section through an area of active upwelling, is the best guide to an interpretation of such movements. Assuming the surface-waters to be under the stress of a wind effective in their offshore transport, the distribution of mass on this section can be interpreted on the basis of the water-movements suggested by the arrows. The convection cell between stations WS 1053 and 1054 marks the boundary between the coastal and oceanic water types, to which reference has already been made, and seems to act like a roller bearing between the two systems of water-movement. Movement of this boundary to the west (left) would be accompanied by an upwelling from about 300 m. depth.

Depths affected by upwelling

The most straightforward method of determining the depth of upwelling is to utilize the T-S diagrams. From these it is possible to determine from what depth in the offshore water the coastal waters originate. On p. 179 it was shown that in the process of uplift from subsurface depths, the coastal waters remained discrete and that a rise in their temperature was the only important change that took place. If then we take the origin of the T-S curve for the coastal waters at the point where it arises from the T-S curve of the offshore water, the depth on the offshore T-S curve will give us a measure of the depth of origin of the coastal water. These depths are set out in Table 9. The first figure shows the depth from which water is elevated to the surface. Where a range of depths are shown the second figure represents the maximum depth affected, but it is not necessarily implied that water is brought from this depth right to the surface. It is normally elevated from this depth to a somewhat lesser depth on the continental shelf.

Table 9. *Depth of upwelling*

Latitude	Survey I (m.)	Survey II (m.)
19° 44′ S.	—	220
23° S.	—	200–230
25° S.	*ca.* 200	275–300
28° 30′ S.	200–350	180–320

CENTRES OF UPWELLING

The recurrence of upwelling in particular localities has been demonstrated by Schott (1931) and Gunther (1936) in the Peru current. In the Benguela current this question has not received so much attention, but Copenhagen (1953) has suggested that seven such localities exist off the South-west African coast. He goes on to correlate these centres with the bottom topography. The position of the centres of upwelling is deduced from a comparison of the coastal temperature with the temperature of an arbitrary latitudinal standard, taken by Copenhagen as the temperature 200 miles from the coast.

Although the 'William Scoresby's' observations are insufficient to apply this method, it is noteworthy that the areas of low surface-temperature (Fig. 7 a, b) were found in more or less the same regions as those outlined by Copenhagen, that is to say: (1) Saldanha Bay to Orange river mouth; (2) north and south of Luderitz Bay and extending to Walvis Bay on survey II; (3) Cape Frio to Cunene river mouth.

A closer examination of the charts, however, shows that the colder water in the vicinity of Orange river mouth lay in 28° S. in survey I, while in survey II it was centred on 29° S. some 60 miles farther south. It is noteworthy also that the 200 m. contour representing the edge of the continental shelf is 50 miles offshore in 28° S., but 90 miles offshore in 29° S. This area of cold water appeared to show no particular correlation with the topography of the sea-bed.

Probably the most that can be said from the present results is that the conditions on survey II, which represent a characteristically active period of upwelling, show that upwelling was most pronounced in the regions: (1) from 29° to 30° or 31° S.; (2) from 28° S. to Luderitz Bay and northwards to Walvis Bay; (3) possibly an additional area from Cape Frio to Cunene river mouth. To the south of 30° S. we have insufficient data to allow any conclusions to be drawn.

INFLUENCE OF THE DIRECTION OF THE COASTLINE

The absence of any pronounced upwelling from Cape Frio southwards to 22° S. while it is present both to the north and south of this area appears to be rather significant when the shape or direction of the coastline is considered. North of Cape Frio, the coastline runs approximately north–south. From Cape Frio to Walvis Bay its direction changes to about 330° to 150° and south of Walvis Bay to about 352° to 174°. With a S.S.W. (202½°) wind, assuming that the drift is 45° to the left of the wind direction, the resultant water-movement in the region between Cape Frio and Walvis Bay would be in the direction 160° to 340° about 10° onshore towards the coast. Clearly, therefore, along this stretch of coastline the effect of the sea-breeze which is S.S.W. in this area would be to pile water against the coast, rather than remove it and create upwelling.

North of Cunene river mouth (17° S.) the coastline bends away gradually in an easterly direction. This marks the northern boundary of the upwelling and it is possible that Schott's suggestion that the replacement flow for water carried offshore by the wind can occur on the surface, without necessitating the vertical circulation of upwelling along this stretch of coast.

The southern boundary of the current which lies at the Cape of Good Hope may also be considered to be an effect of the direction of coastline relative to the wind direction.

SEASONAL VARIATION OF UPWELLING

The observations made by the 'Willlam Scoresby' cannot alone be regarded as illustrative of seasonal variation of the current. The overall lower temperatures and greater wind and upwelling during survey II, while probably characteristic enough of winter conditions, could no doubt be found at least to some extent at almost any time of the year in suitable meteorological conditions. It is, therefore,

more desirable to look upon the difference between the two surveys as an example of the current in two phases—at survey I a quiescent phase subsequent to upwelling, and at survey II a phase of active upwelling.

It is very difficult to determine how much the upwelling varies throughout the year. Clearly it is a phenomenon which can occur at all seasons. Schott (1902), Franz (1920) and Bobzin (1922) have all endeavoured to make estimates of the intensity of upwelling at different seasons.

Schott based his estimate on the extent of the upwelling zone and a comparison of the temperature of the inshore waters with that of the offshore waters at a distance of about 300 km. from the coast, and he agrees with Franz in placing the maximum period of upwelling in August and the minimum in summer. Schott, however, put the minimum in November and Franz in February. Bobzin, on the other hand, derived his estimate from a comparison of the mean monthly and mean yearly temperatures and their mean variation, and this led him to conclude that upwelling reached its maximum in summer (October–December) and its minimum in June.

Bobzin ascribed the discrepancy between his results and those of Schott and Franz to the effect of solar heating of the upwelled water, which would be at its greatest in summer and at its minimum in winter, thereby masking the true changes of temperature due to upwelling. The criteria used by Bobzin to estimate the upwelling are based on somewhat abstract considerations. Moreover, his conclusions are based on a large number of temperature observations taken at Swakopmund and Luderitz Bay—only two points on a coastline some 1000 miles in length. It seems doubtful, therefore, whether Bobzin's 'Relatives Mass des Auftreibbewegung' produces any more accurate a picture than derived by Schott and Franz.

On the assumption that wind is the primary cause of upwelling, then we may consider the winds to be as good a measure as anything else of the frequency of upwelling. In winter the trade winds are slightly stronger than in summer, and one might expect a consequent intensification of the relative current in winter. On the other hand, it is evident from Fig. 5 that the coastal winds reach their greatest upwelling effect in that season. Clearly the crucial point is the relative effect of the trade wind and the coastal wind, but without more detailed observations we can go no further.

NON-CONSERVATIVE PROPERTIES

The distribution of dissolved oxygen

Since dissolved oxygen is related to the biological process in the sea, its distribution is governed not only by water-movements and interchange with the atmosphere, but also by the varying biological activity in the water masses.

The oxygen content (Figs. 38–44) usually reaches its maximum concentration in the surface-layers of the sea as a result of atmospheric exchange and the photosynthesis of the phytoplankton in these layers. Beneath the surface-layers the oxygen content decreases towards the sea-bed. Normally in sea-waters the oxygen content remains fairly high in the deeper layers, but off South-west Africa there is a very rapid decrease with depth in the inshore waters, so that even in normal conditions in this region a content of less than 1 ml. O_2/l. is found in the vicinity of the sea-bed on the continental shelf. The sections from survey II (Figs. 41–4) show that the layer of low oxygen slopes upwards towards the surface as the coast is approached. Furthermore, it extends beyond the edge of the continental shelf, producing a layer of minimal oxygen content adjacent to the continental slope, at depths of about 400 m. on survey II.

On survey I this layer of minimal oxygen is much more pronounced, not only offshore, but also inshore where it extends to the sea-surface at the coastal station WS 981 off Walvis Bay (Fig. 40).
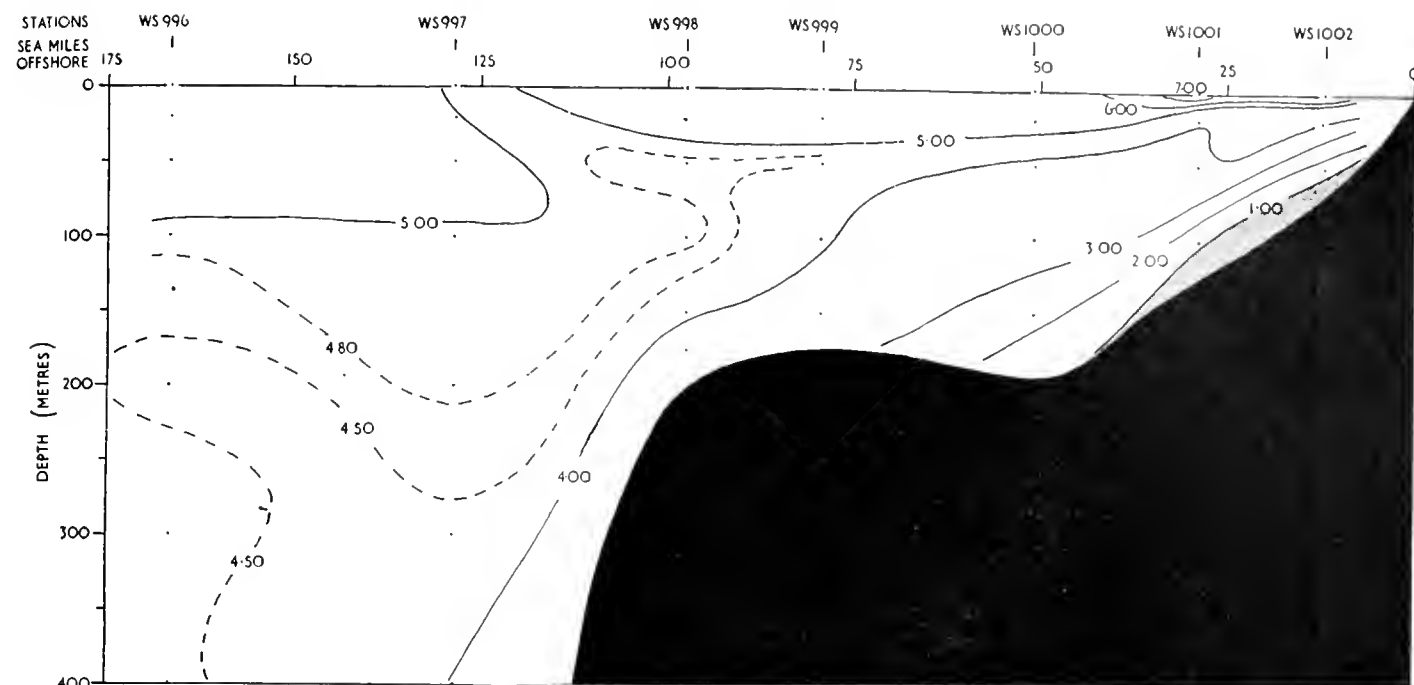
Fig. 38. Distribution of dissolved oxygen. Section off the mouth of Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.
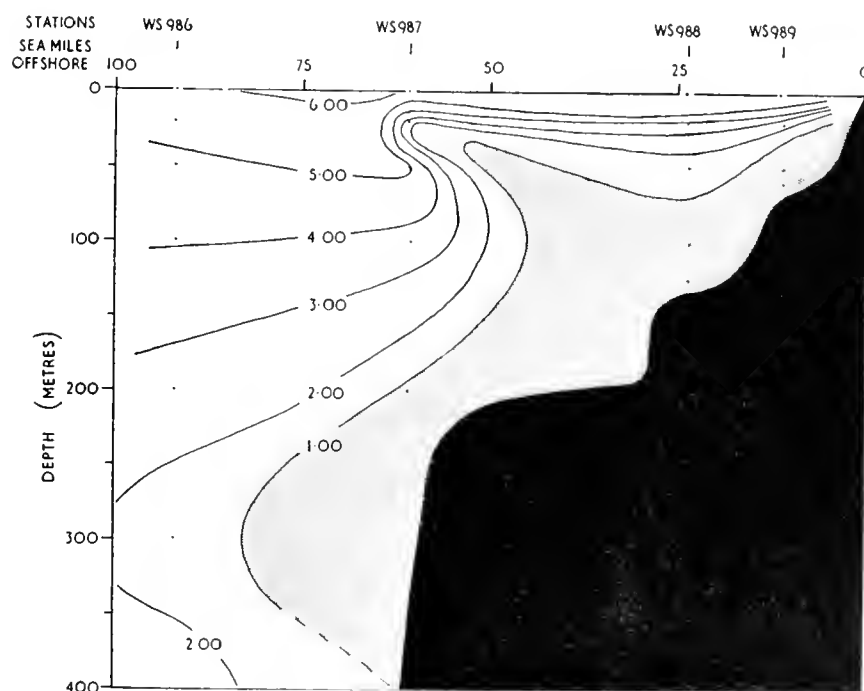
Fig. 39. Distribution of dissolved oxygen. Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of stations are shown in Fig. 1.

Here, even with a recorded phytoplankton population of more than 10^7 cells (Table 14) the surface-water was only 5·8% saturated with oxygen (cf. Steeman-Nielsen, 1957, p. 75).

A comparison of the oxygen sections with those of temperature and salinity shows that the low oxygen content exhibits features of distribution similar to those of the upwelling water. Therefore
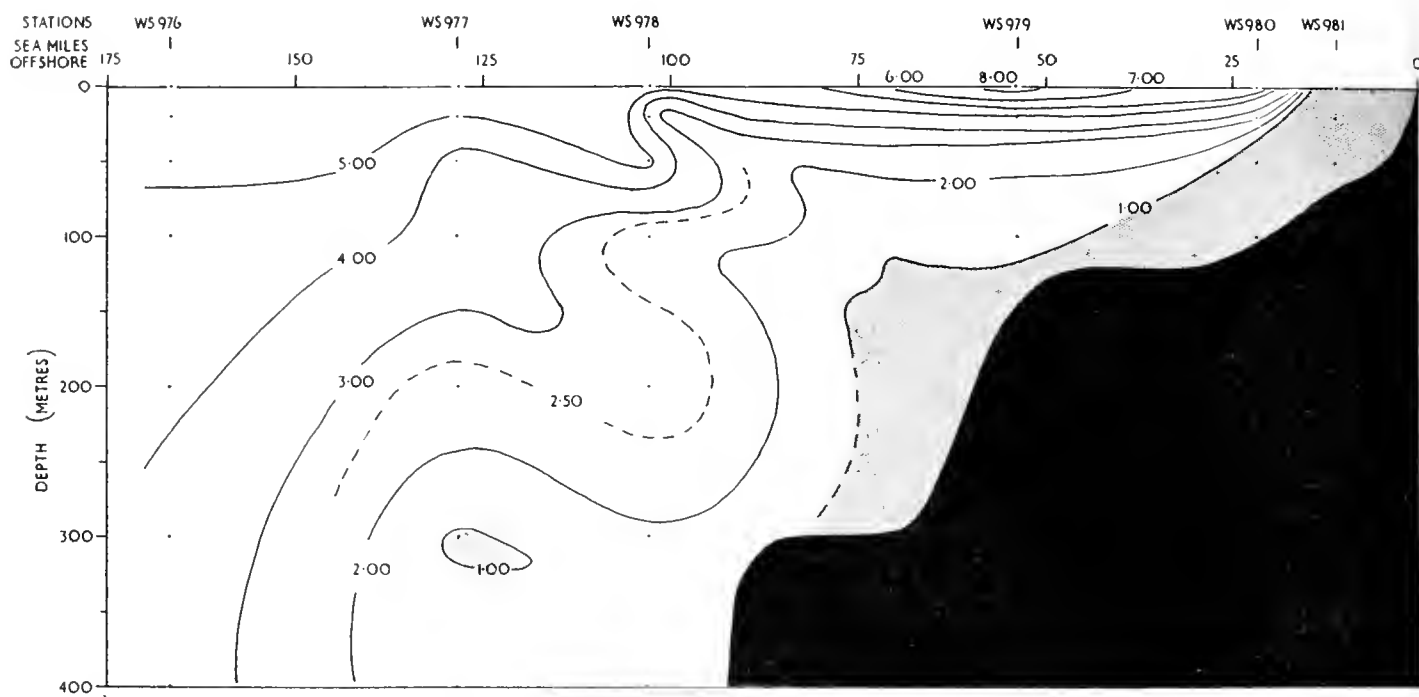
Fig. 40. Distribution of dissolved oxygen. Section off Walvis Bay, 6–8 March 1950, survey I.
Positions of stations are shown in Fig. 1.
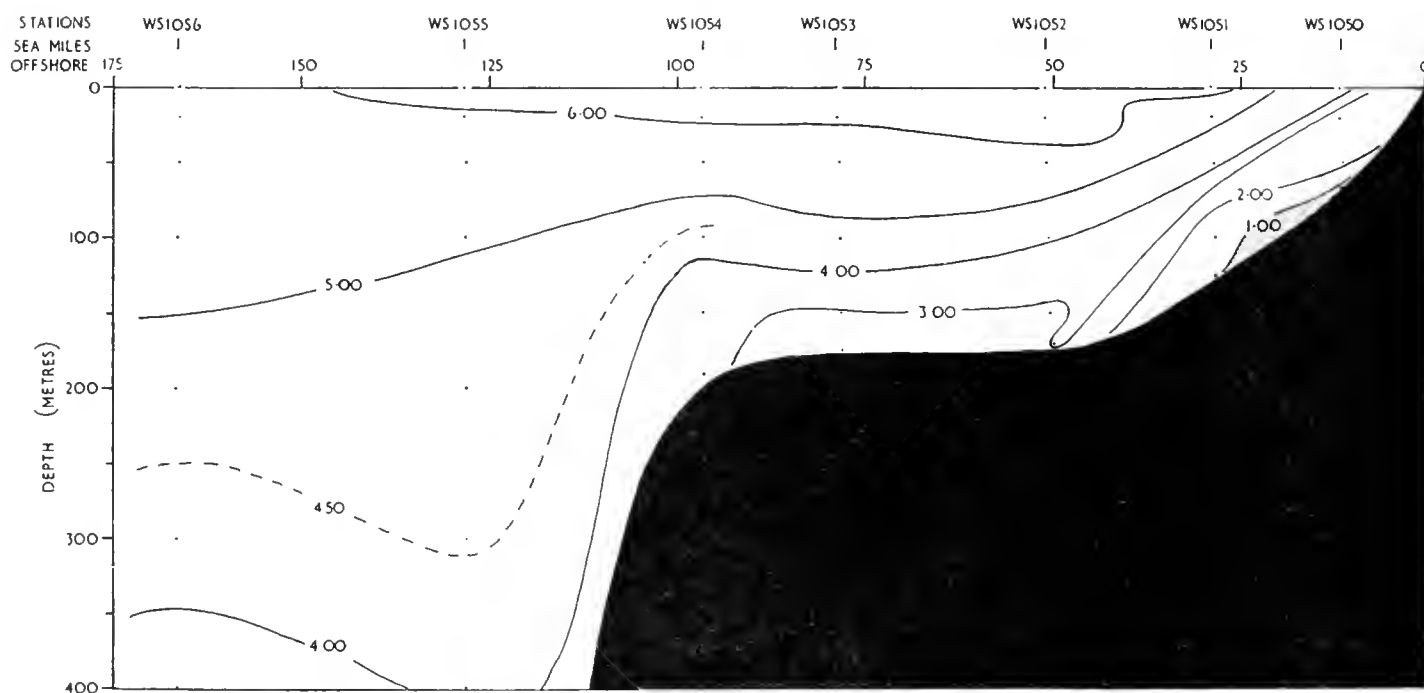
Fig. 41. Distribution of dissolved oxygen. Section off the mouth of Orange river, 21–24 September 1950,
survey II. Positions of stations are shown in Fig. 2.

to trace its origins let us first examine the waters at subsurface depths adjacent to the continental
shelf, from which the upwelling occurs.

If we plot the dissolved oxygen content against temperature for survey I in the 200–600-m. layers
(Fig. 45), we see that the stations closer to the continental shelf and to the north of the region have
the lowest oxygen content, while those farther offshore and in the south have a higher oxygen content.
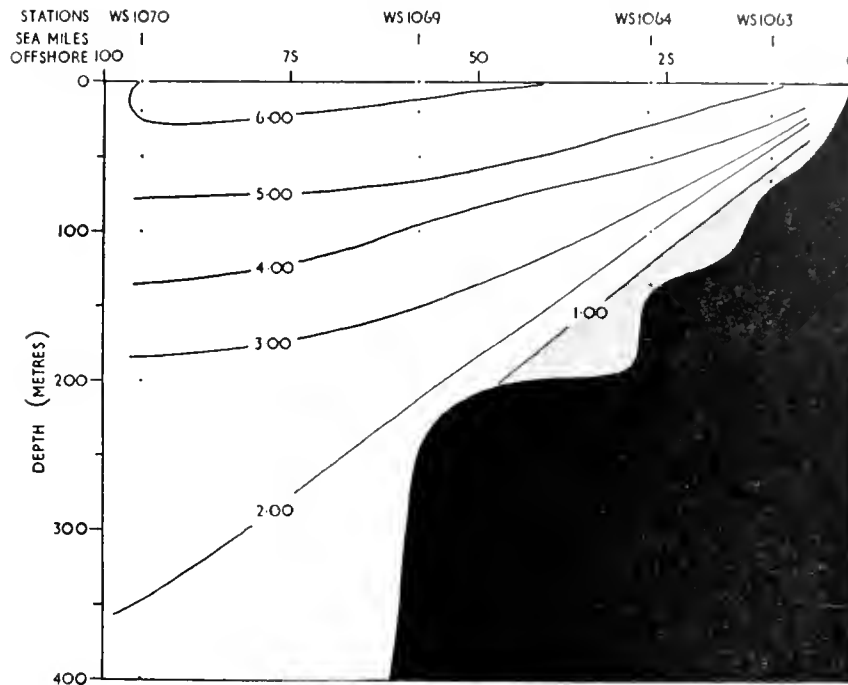
Fig. 42. Distribution of dissolved oxygen. Section off Sylvia Hill, 25-27 September 1950, survey II.
Positions of stations are shown in Fig. 2.
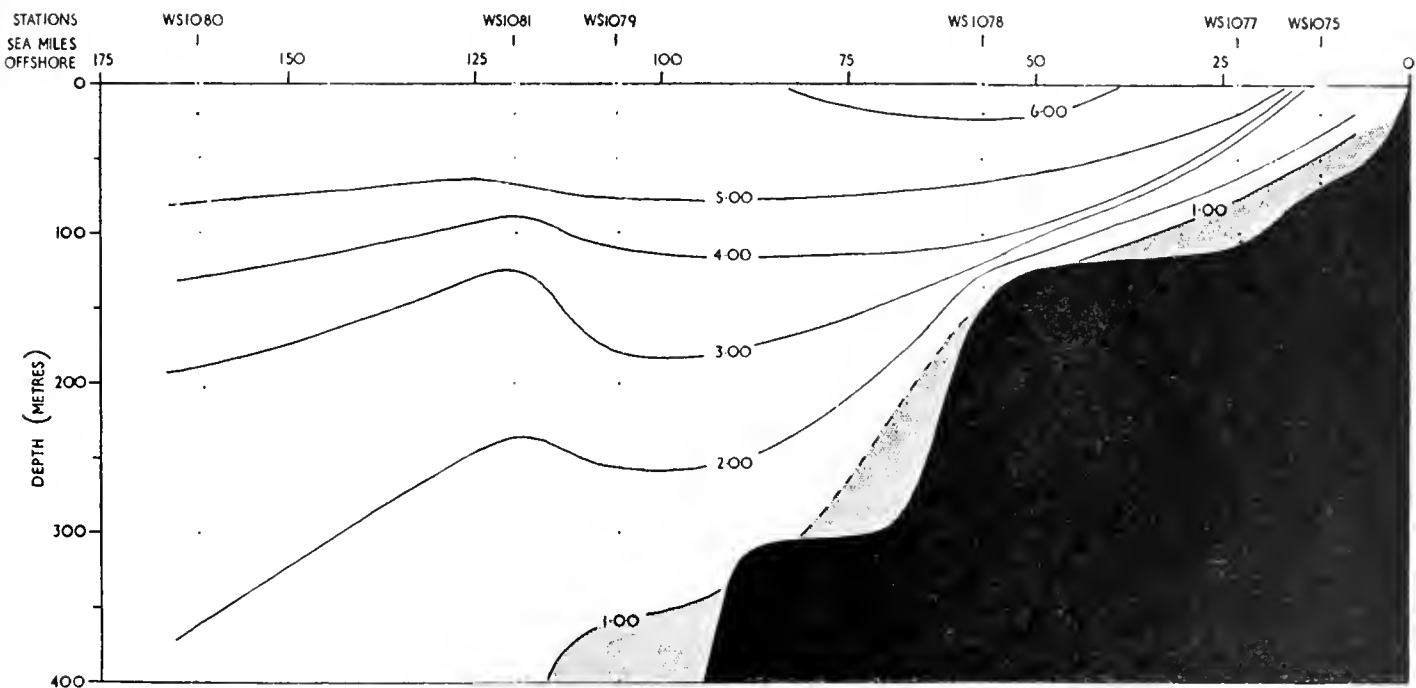
Fig. 43. Distribution of dissolved oxygen. Section off Walvis Bay, 29 September–3 October 1950, survey II.
Positions of stations are shown in Fig. 2.

It was suggested on p. 183 that the water against the edge of the continental shelf at these depths exhibited a southerly movement, and therefore it is interesting to amplify our own results from some stations of the 'Meteor' (Wattenberg, 1933) to the north and south of the region. These are plotted in Fig. 46 and show a still wider contrast between the stations in the north and in the south. The positions of the 'Meteor' stations are shown in Table 10. The two curves from the 'Meteor' stations
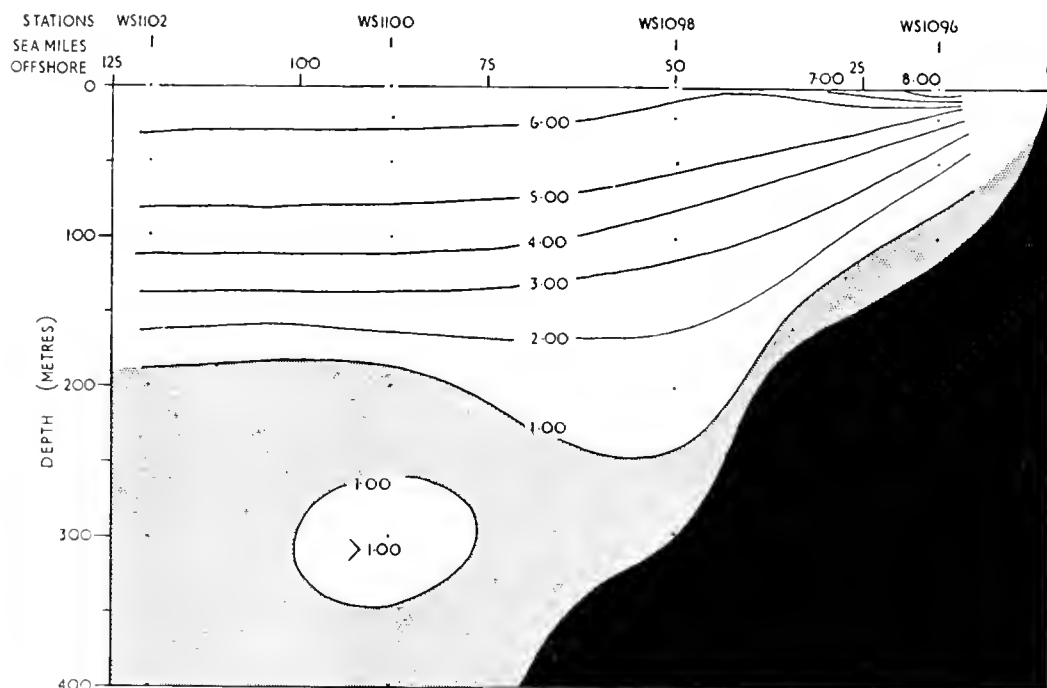
Fig. 44. Distribution of dissolved oxygen. Section off Möwe Point, 9–11 October 1950, survey II.
Positions of stations are shown in Fig. 2.
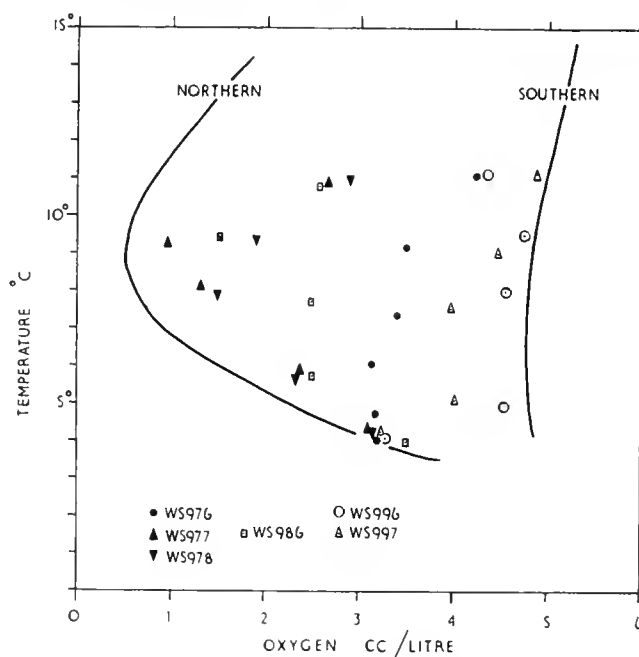
Fig. 45. Temperature and oxygen in the 200–600 m. layer at the 'William Scoresby' stations, survey I. Positions of the stations are shown in Fig. 1. The two heavy lines are taken from Fig. 46, and show the temperature/oxygen relationships in this layer to the north and south of the area surveyed, compiled from selected 'Meteor' stations.

are reproduced in Fig. 45 and show that the 'William Scoresby's' observations lie in between these two curves, the stations in the north and closer to the continental shelf lying near to the curve for the 'Meteor's' northern stations.

The decrease in oxygen content at the northerly 'Meteor' stations between 8° and 12° C. represents the layer of minimal oxygen content which extends across the tropical South Atlantic ocean (Fig. 47). This layer Riley (1951) has shown to result probably from the balance between the rates of decomposi-

tion of detrital organic matter falling from the shallower layers, and the rate of renewal of oxygen by turbulent processes.

If, therefore, the indication of southerly movement along the edge of the continental shelf at these depths is real, such a movement would carry this oxygen-depleted layer into the region of the Benguela current in this depth horizon. The water bounding such a current to the west as shown by the offshore stations has a higher oxygen content which can be ascribed to water of the type shown by the 'Meteor' southern stations.
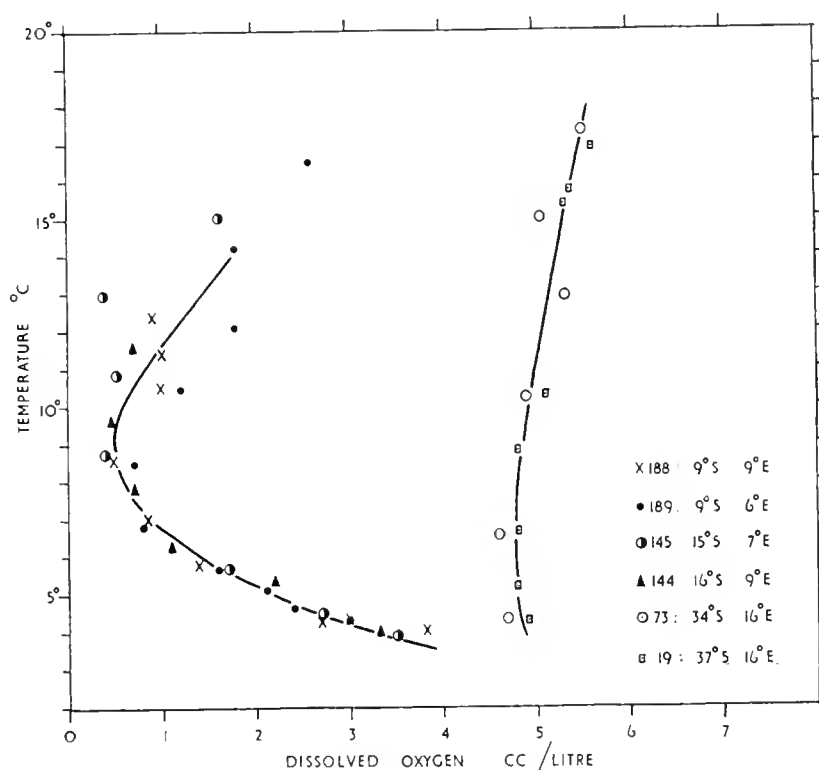
Fig. 46. Temperature and oxygen in the layer of minimum oxygen at selected stations of the 'Meteor' expedition, to the north and south of the area surveyed by the 'William Scoresby'. The positions and dates of these stations are given in Table 10.

With subsequent upwelling it might be expected that the water uplifted to the surface would be heavily depleted in dissolved oxygen and this the more so the farther north in the region. The presence of this water on the continental shelf would accentuate the effects of local decomposition of organic matter on the sea-bed, and consequently the depletion of oxygen would become more accentuated towards the coast on the continental shelf. This proceeds to such an extent that anaerobic conditions are created on the sea-bed (p. 204).

Table 10. *Positions of the Deutsche Atlantische Expedition 'Meteor' stations used in the construction of Fig. 46*

Station no.	Position	Date
19	36° 40′ S., 16° 22·5′ E.	11. vii. 1925
73	34° 02′ S., 15° 48′ E.	12. xi. 1925
144	16° 03·5′ S., 09° 29′ E.	4–5. v. 1926
145	15° 16·5′ S., 06° 32·6′ E.	6. v. 1926
188	08° 58′ S., 08° 57·7′ E.	5. ix. 1926
189	09° 00′ S., 06° 00′ E.	6. ix. 1926
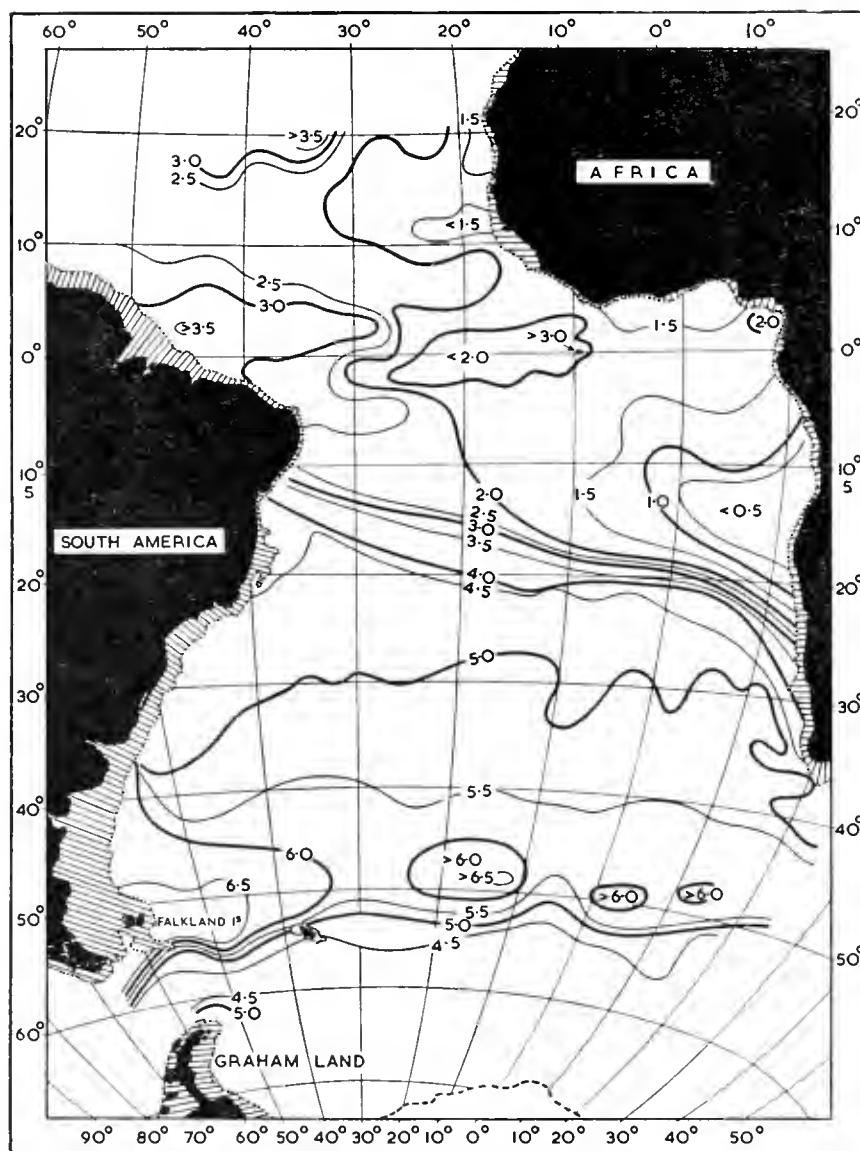
Fig. 47. The distribution of the layer of minimum oxygen in the South Atlantic Ocean. From Wiss. Ergebn. dtsch. Atlant. Exped. 'Meteor', Bd. IX, Beil. XXXVII. This figure shows the oxygen content at a depth of 300 m.

NORMAL AND ABNORMAL CONDITIONS WITHIN THE CURRENT

A comparison of the dissolved oxygen sections for survey I and survey II (Figs. 38–40 and 41–4) shows that the oxygen depletion on the continental shelf was much more pronounced during survey I, and in particular in the Walvis Bay region where even at the sea-surface inshore (WS 981) the oxygen content was only 0·33 c.c. O_2/l. The consequences of such an immense depletion of dissolved oxygen are discussed later (p. 199) in the consideration of its effects upon fish mortality, but for the present we must consider what conditions lead up to such a catastrophic event.

The maintenance of aerobic conditions on the continental shelf must be dependent to a great extent upon the renewal of oxygen by turbulent processes. In this case one would expect, as indeed is shown by the results of survey II, that in the conditions which set up a strong northerly current the introduction of more highly oxygenated water would be at its maximum, and the oxygen on the continental shelf would probably be continually renewed.

But if the currents were slowed down, stopped or even reversed, then the converse might be expected to occur. The turbulent renewal of oxygen would be at its minimum, the effects of decomposition on

the anaerobic sea-bed would become magnified, and the production of hydrogen sulphide by the sulphate-reducing bacteria in the bottom sediments (p. 204) would assist in the depletion of oxygen.

The conditions found at Walvis Bay on survey I exemplify this. The previously upwelled waters, warmed and mixed with the influx of oceanic water, may be considered to have produced almost stagnant conditions in this region, and some few days before our arrival in Walvis Bay a small mortality of fish was observed by the local inhabitants.

The meteorological records (Fig. 35 and Table 3) show that, prior to our arrival in Walvis Bay, there had been a predominance of calm and northerly winds for at least four or five weeks. It is highly probable that adverse weather conditions such as these must be responsible for the occurrence of such conditions of stagnation as are eventually associated with fish mortality.

These abnormal conditions always occur in the summer (Copenhagen, 1953) during which time northerly winds predominate at Walvis Bay. This fact is not shown to advantage in Fig. 5, probably
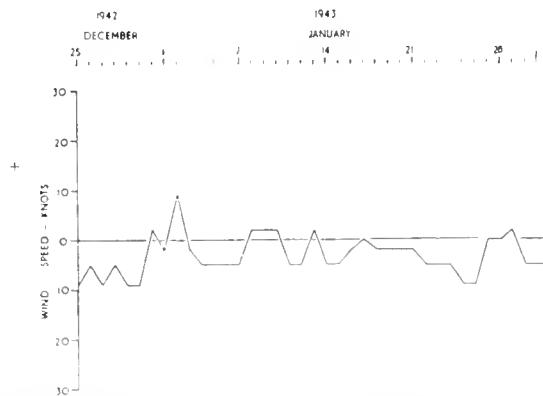
Fig. 48. Predominant wind vectors at Walvis Bay during the fish mortality of the summer of 1942/3. The wind vectors are plotted in the same manner as in Fig. 35. From the records of the climatological station at Walvis Bay.

because these winds represent rather exceptional circumstances, and they do not necessarily occur in every year. Other opportunities do occur, however, of comparing these abnormal conditions with meteorological records.

In January of 1943 a considerable mortality of fish was reported by Dr McConnel at Walvis Bay (Brongersma–Sanders, 1948). It extended from Walvis Bay to Concepcion Bay, a distance of some 60 miles along the coast.

At this time hourly meteorological observations were taken at Walvis Bay. The winds recorded there are plotted (Fig. 48) in the same manner as in Fig. 35, any winds between south-west through south to east-south-east being counted as positive and all other winds as negative. The negative winds, mainly north to north-west, are those which would have been conducive to the abnormal conditions, and Fig. 48 shows that they persisted throughout January 1943.

A mortality of much greater extent occurred in the summer of 1924–5 (Reuning, 1925) and the wind records from Walvis Bay (Fig. 49) again show that after the end of December conditions would have been favourable for the production of abnormal conditions.

One further example is a smaller mortality observed at Walvis Bay in December 1925, and throughout this month the winds were either northerly or calms.

There appears, therefore, to be a well-defined correlation, at least between the occurrence of fish mortalities and the spells of calm weather or northerly winds, which create abnormal conditions in the vicinity of Walvis Bay.
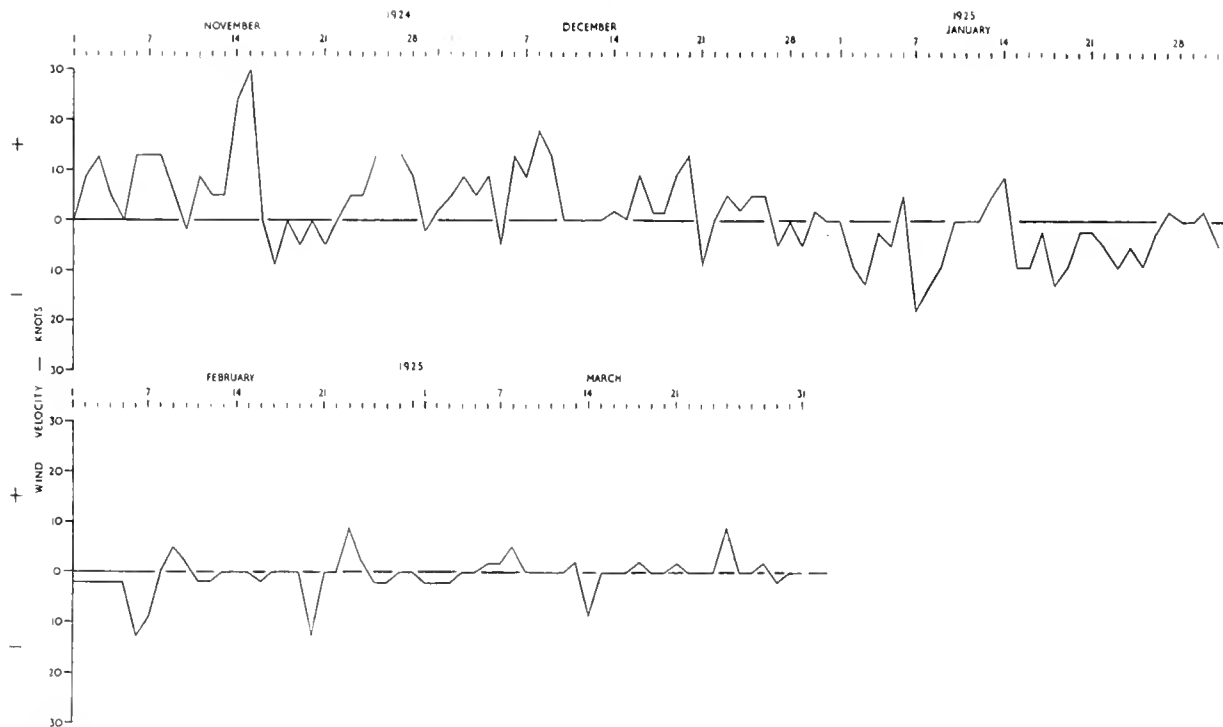
Fig. 49. Wind vectors at Walvis Bay preceding and during the fish mortality in the summer of 1924/5. The wind vectors are plotted in the same manner as in Figs. 35 and 48. From the records of the climatological station at Walvis Bay.
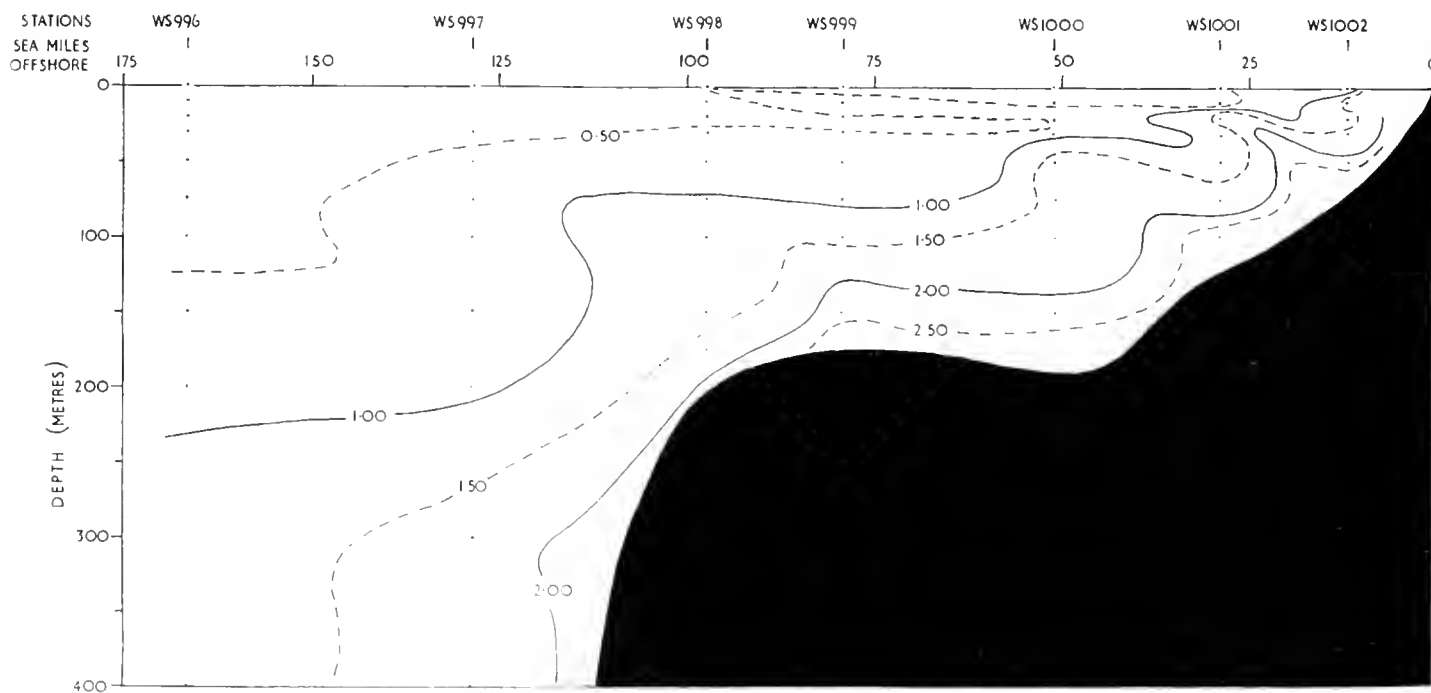
Fig. 50. Distributions of phosphate (mg. ats. P/m.^{3}). Section off the mouth of Orange river, 12–14 March 1950, survey I. Positions of stations are shown in Fig. 1.

The distribution of dissolved inorganic phosphate-phosphorus

The sections showing the distribution of inorganic phosphate (Figs. 50–6) indicate that on both surveys the pattern of distribution is essentially similar.

The lowest phosphate concentrations are found in the oceanic surface-waters, where from a com-
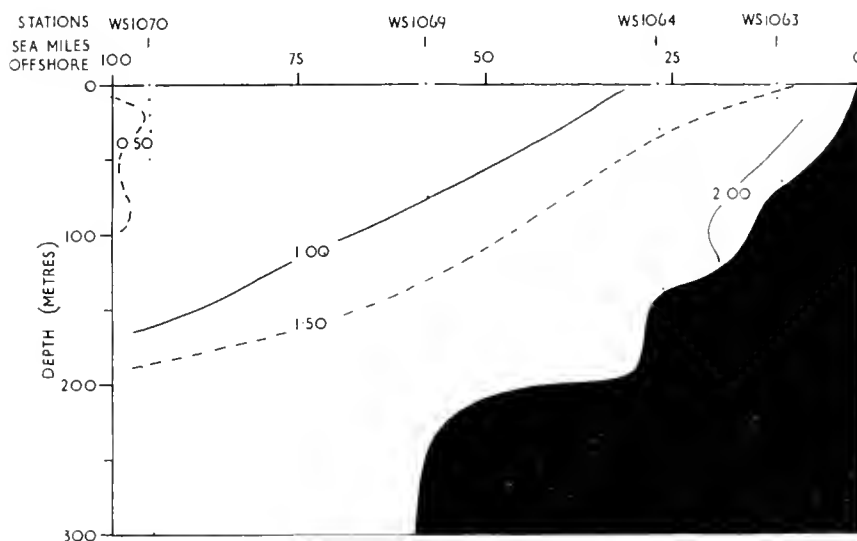
Fig. 51. Distribution of phosphate (mg. ats. P/m.^{3}). Section off Sylvia Hill, 10–11 March 1950, survey I. Positions of stations are shown in Fig. 1.
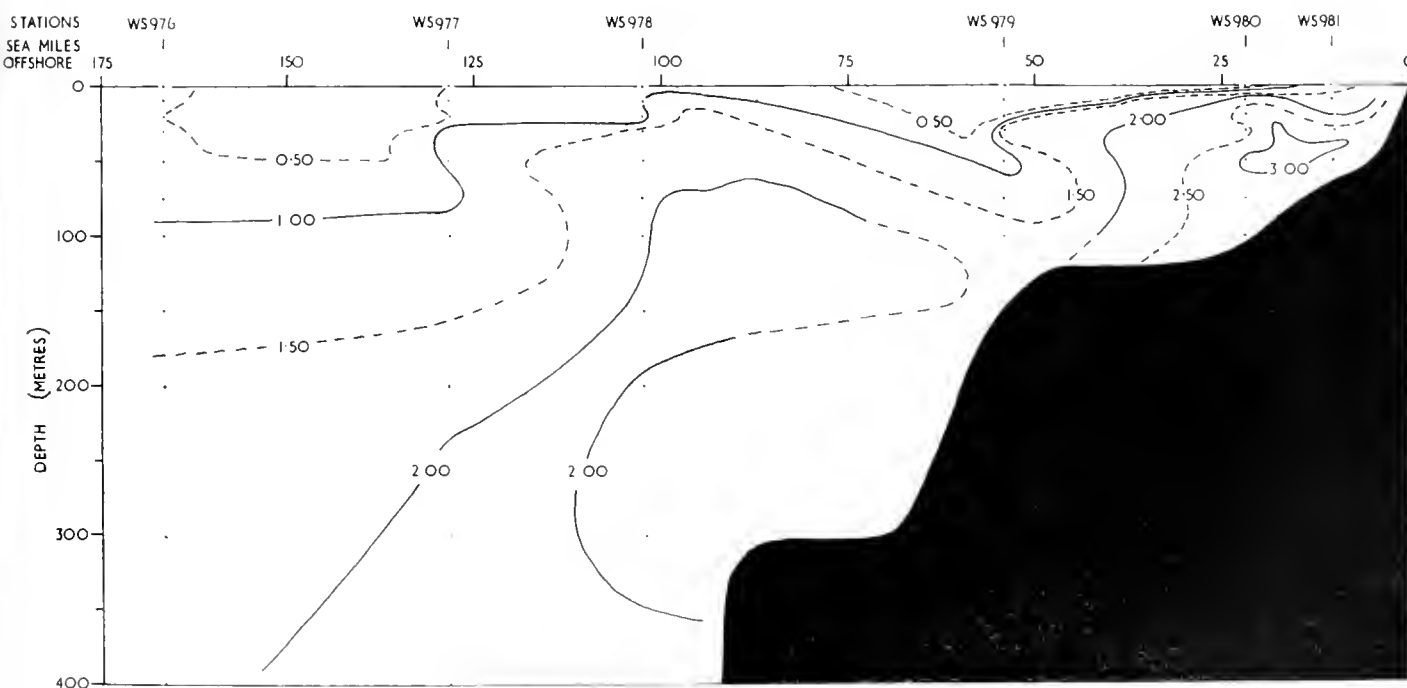
Fig. 52. Distribution of phosphate (mg. ats. P/m.^{3}). Section off Walvis Bay, 6–8 March 1950, survey I. Positions of stations are shown in Fig. 1.

plete absence of phosphate values of up to 0·5 mg. ats. P/m.^{3} were found. The upwelled coastal waters present a sharp contrast. In them the phosphate content is very high, on occasion reaching more than 2·0 mg. ats. P/m.^{3}.

Below the surface-waters the phosphate concentration increases down to the sea-bed inshore and

to greater depths offshore. In places there is a layer of maximal phosphate off the edge of the continental shelf. This coincides approximately in depth with the layer of minimal oxygen, but like the maximal phosphate layer in the equatorial parts of the ocean, it is much less well defined than the
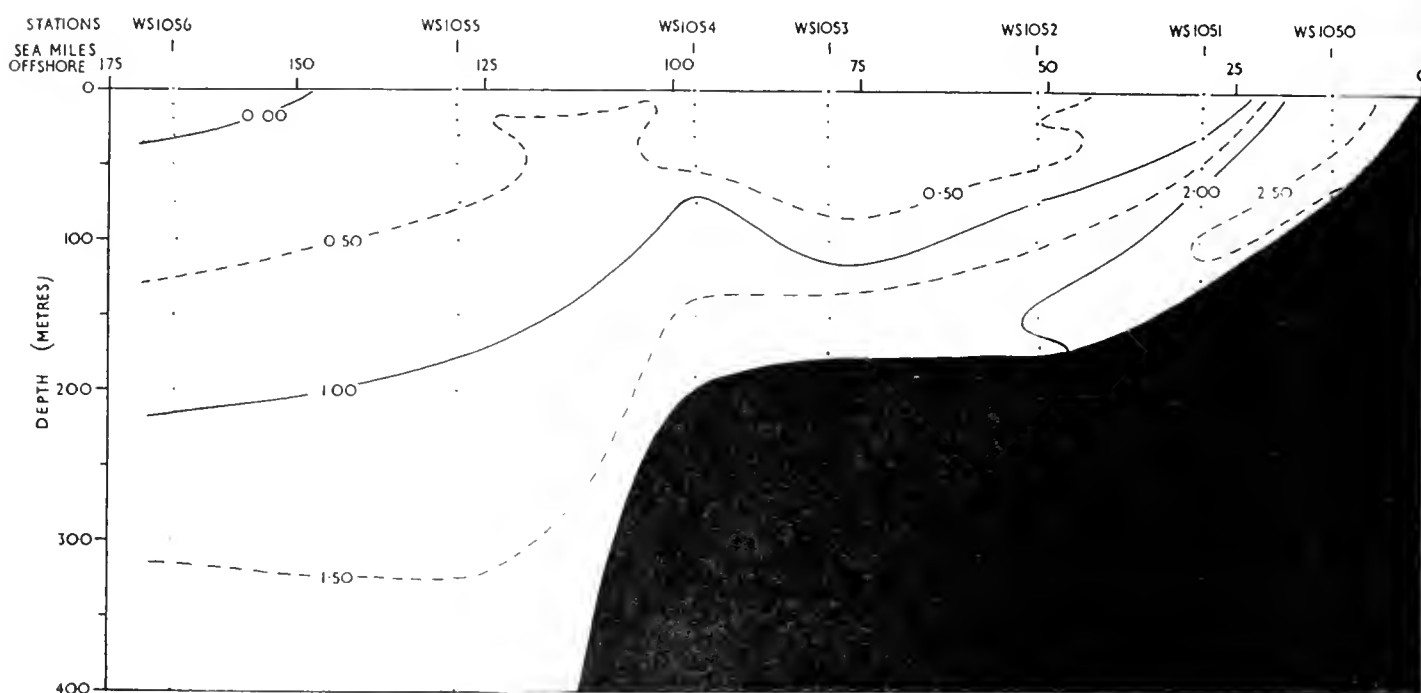
Fig. 53. Distribution of phosphate (mg. ats. P/m.³). Section off the mouth of Orange river, 21–24 September 1950, survey II. Positions of stations are shown in Fig. 2.
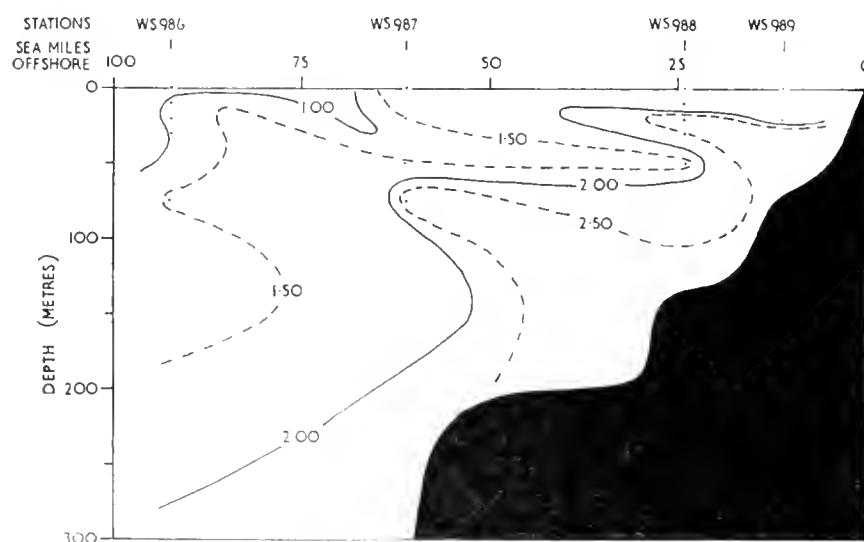
Fig. 54. Distribution of phosphate (mg. ats. P/m.³). Section off Sylvia Hill, 25–27 September 1950, survey II. Positions of stations are shown in Fig. 2.

oxygen minimum layer, and the phosphate concentration more often increases almost regularly to greater depths. The maximum concentration is reached in the antarctic intermediate water.

In the layer of minimal oxygen, however, the inorganic phosphate concentration reaches values of about 2·0 mg. ats. P/m.³ With upwelling, this extremely phosphate-rich water is brought up on to the continental shelf, where it provides the necessary nutriment and permits the growth of the heavy crops of phytoplankton in the coastal waters. In several of the sections it will be apparent that the
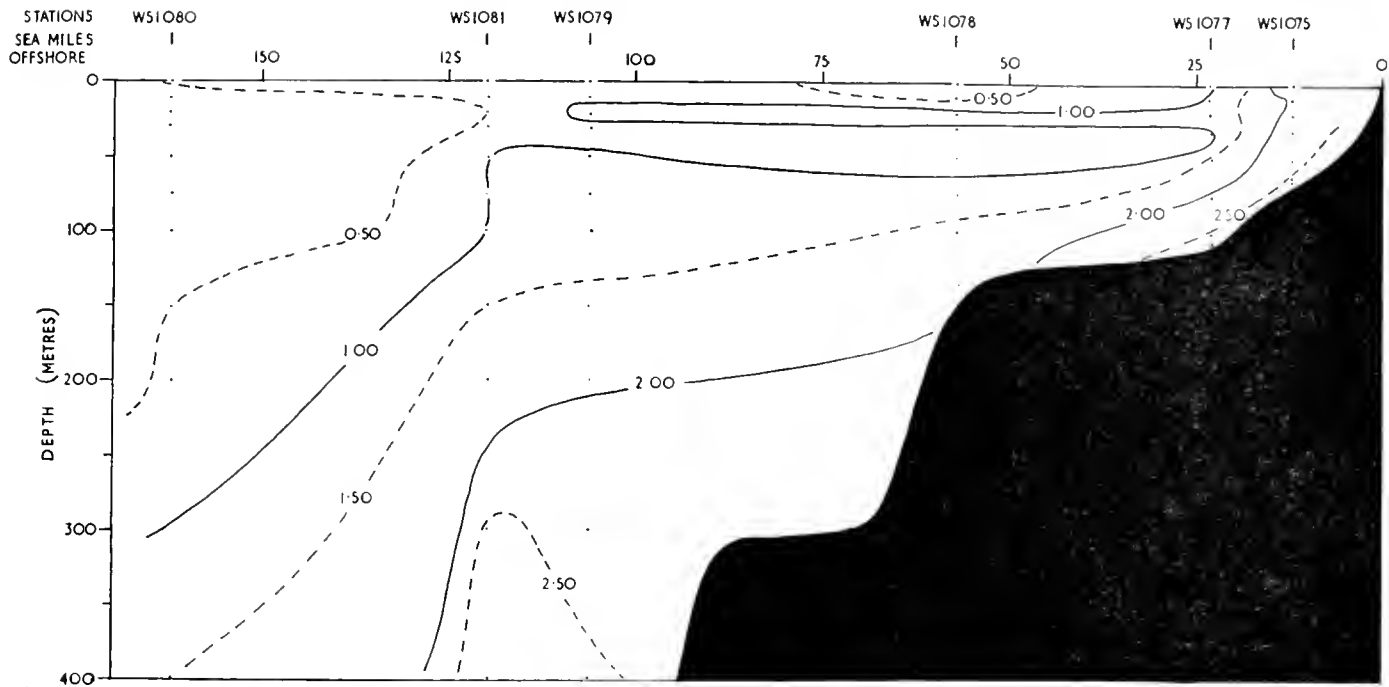
Fig. 55. Distribution of phosphate (mg. ats. P/m.³). Section off Walvis Bay, 29 September–3 October 1950, survey II. Positions of stations are shown in Fig. 2.
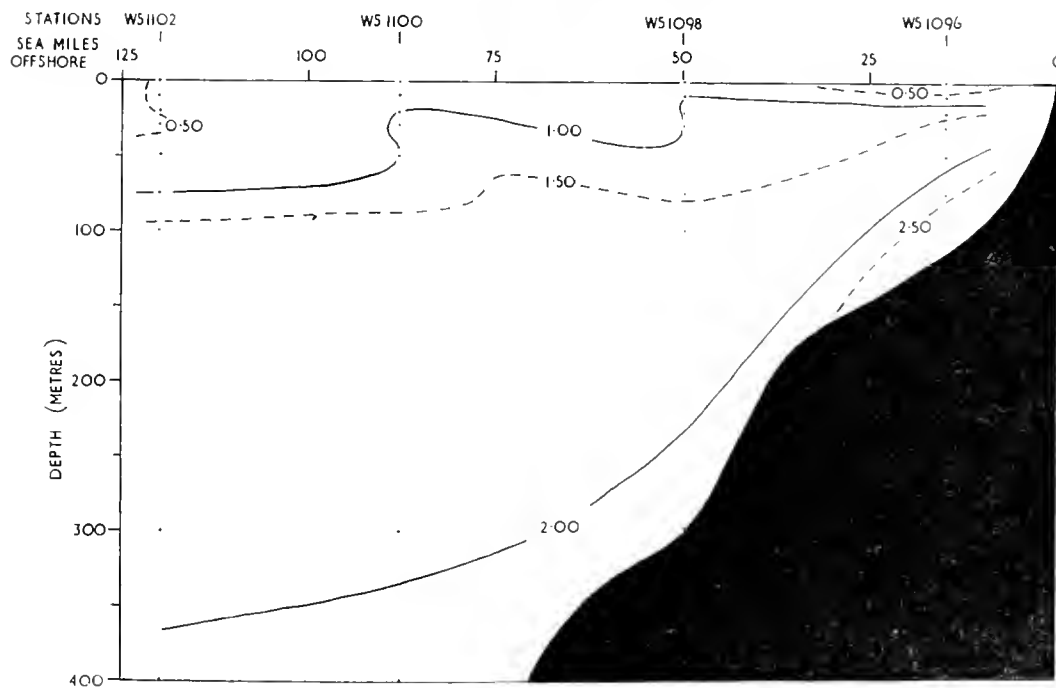
Fig. 56. Distribution of phosphate (mg. ats. P/m.³). Section off Möwe Point, 9–11 October 1950, survey II. Positions of stations are shown in Fig. 2.

phosphate concentration on the continental shelf is higher than that in the water which is being upwelled, and one must attribute this to further enrichment by local decomposition of organic matter on the shelf.

On the Orange river line of survey II (Fig. 53) there is a divergence of phosphate-rich water towards the surface at the edge of the continental shelf. This corresponds with the diverging current which was postulated from the isosteres on this line of stations (Fig. 37).

BOTTOM DEPOSITS

One of the most interesting features of the South-west African region is the presence, on the sea-floor of the continental shelf, of an extensive area of diatomaceous mud. In contrast to the great deposits of diatom ooze which occur in the deep ocean, this zone is confined to shallow waters, and by its very proximity to the sea-surface has made its periodically catastrophic effects all the more evident.

The extent of the diatom mud was outlined by Marchand (1928). He described it as extending principally from 21° 30′ S. to 24° 30′ S. (a distance of about 200 miles) and running seawards for some 25–30 miles from the coast. The bottom samples from this area in his words 'have a green colour and are of a muddy or clayey consistency. The stench emanating from them is unbearable and somewhat similar to hydrogen sulphide or the odour characteristic of putrefaction.'

Close to the coast, however, this mud was not found, and Marchand says that it gives place to a belt of grey sand on which the marine fauna and flora were abundant. It appears, therefore, that the evil smelling mud was confined to an area of the sea-bed between depths of about 50 and 150 m., extending along the coast for some 200 miles.

The absence of marine life in this diatom mud, and the uselessness of the ground for trawling, led to the name by which it is now known, the 'azoic zone' (strictly speaking the name 'anaerobic zone' would be more precise, for the mud does in fact support bacteria and is, therefore, not 'azoic').

Copenhagen (1934) examined the deposits in the azoic zone closely and concluded that the evil smell was in fact hydrogen sulphide, and that it originated from the activities of sulphate-reducing bacteria (Butlin, 1949) which were shown to be present in the sediment. Analyses of the sediment revealed a high content of organic matter and, on drying, a whitish-yellow deposit, evidently of sulphur, became apparent on the surface of the mud.

Microscopical examination of the sediment has shown it to be composed mainly of diatom frustules, although towards the seaward limit of the zone foraminiferal remains become increasingly abundant (Marchand, 1928).

The importance of the azoic zone in the circulation of the waters of the Benguela current became evident when the results of survey I were examined. It was decided, therefore, on survey II to include a series of bottom sampling stations in an attempt to delineate more clearly the total extent of the zone. Samples were taken to the south and to the north of the limits noted by Marchand (1928), and these have shown that the azoic mud extends, at least patchily, for some 400 miles along the coast, from Cunene river mouth (17° 30′ S.) in the north, to about 25° S. Seawards of the deposit is a fairly rapid change to the stone-grey globigerina ooze which characterizes the sediments of the continental slope and floor of the deep ocean to the west.

It is particularly interesting, however, that the azoic mud was not found on the Orange river line, nor in the trawl at station WS 990 on survey I, and this suggests that the southern limit must indeed be somewhere in the region of 25° S. The sediments on the shelf south of the azoic zone do not differ markedly in appearance from the azoic mud, but they have none of the offensive smell of the latter.

Reference to Figs. 38 and 41 shows that over this area the oxygen content of the water overlying the sea-bed, exemplified by the Orange river line, was by no means so depleted as that found, for example, off Walvis Bay over the azoic zone (cf. Figs. 40 and 43). This, in turn, relates to the higher content of dissolved oxygen in the water which was being upwelled on the Orange river line (as shown by the oxygen content at 200–300 m. off the edge of the continental shelf) as compared with that upwelling further to the north.

The evidence, therefore, points strongly to the probability that this diatomaceous sediment to the

south of the azoic zone is maintained in an *aerobic* state by the circulation over it of upwelled water which is not heavily depleted of oxygen.

Another factor, however, which must be considered is that the northerly winds and calms experienced at Walvis Bay (p. 199) do not appear to prevail on the stretch of coast south of 25° S., and their absence may ensure a free circulation of the current over the sediment; but it is felt that these meteorological conditions may concern more implicitly the intensity of the development of the anaerobic region rather than determine the presence or absence of such a zone.

The presence of anaerobic conditions is essential for the growth of sulphate-reducing bacteria, and if the sediment is kept oxygenated they cannot survive.

We have already seen (p. 198) how particular conditions within the current may magnify the effects of hydrogen sulphide production, and indeed at times it is even evolved actively from the sea-surface. There are many observations of bubbles of the gas rising to the sea-surface, but perhaps the following newspaper account gives the most graphic description! (*News Chronicle*, 1938):

SEA GAS ATTACKS TOWN

Swakopmund, the small coastal town in South-west Africa, is undergoing a gas attack set up by continuous submarine disturbances. Heavy sulphurous fumes, especially towards evening, are penetrating as far as 40 miles inland.

EFFECT. Atmosphere like a London fog, metalwork turned black, public clocks blotted out by deposit, thousands of fish strewn on beach, sharks come into surf gasping on evening tide.

CAUSE. A geologist, discounting volcanic action, says sulphuretted hydrogen, produced by bacteria on the sea floor from calcium sulphate or gypsum, accumulates until it raises islands of mud, which eventually burst.

In 1951 a particularly active disturbance took place, and on 16 February the *Bulawayo Chronicle* (Anon., 1951*a*) reported:

SEA ERUPTIONS OFF SOUTH-WEST AFRICA

Swakop. S.W.A. Thurs.

The stench of sulphurous sea eruptions pervades the air day and night. Buildings which were white yesterday, are discoloured and black today.

Dead fish are being washed up along the beaches for over 100 miles to the north from Swakopmund. They include many strange species, such as sea snakes and eels, which are found only occasionally when the sea bottom of their habit undergoes violent disturbance.

The sea appears to be boiling with bubbles rising to the surface, but the temperature of the water is only 60°–70° F.

These eruptions continued through March and three mud islands were thrust up in Walvis Bay (Anon., 1951*b*). The largest, about 100 yards long, disappeared overnight.

The islands were similar to one which was thrust up in 1900. Waldron (1910) reported on the latter, from which samples were taken by an officer of a regiment at Walvis Bay, who swam out to the island. The samples were typical of the mud lying on the sea-bed in the bay, and the temperature of the water remained low in spite of the fact that 'steam' was observed to issue from the northern side of the island. The appearance of the island was accompanied by a very strong smell of hydrogen sulphide. As yet no satisfactory explanation of the formation of these islands has been reached.

The importance of the sediment of the azoic zone in yet another way has been emphasized by Brongersma–Sanders (1948) who has shown the significance of this anaerobic deposition of organic matter to oil geology. It is noteworthy how closely the conditions of deposition within this upwelling current parallel those found associated with fossil deposits.

Study of this diatomaceous mud—first distinguished by Neaverson (1934) from the nearly colourless diatomaceous ooze of some deep-sea deposits—may also yield interesting evidence on the silicate

cycle in the sea, by comparison and contrast between the diatom populations found living in the area (the biocoenosis) and the assemblage of forms found in the deposit (the thanatocoenosis). The problems that this type of work may help to solve may even include evidence as to the speed of subsurface currents, as may be seen from the brilliant exposition by Kolbe (1957) working on more specialized samples from very deep waters (cores taken during the Albatross Expedition).

Preliminary examination of our samples from the Walvis Bay line already suggests striking differences between the bottom deposits and the plankton. Of the forms remaining recognizable in the deposits a vastly greater proportion belong to the Discoidae than have yet been recorded in any of the numerous plankton samples from the area of which analyses are now available. That this may be due to much more rapid re-solution of the less strongly silicified forms has been suggested previously on the basis of work in other diatom-rich waters (Hart, 1934, 1942).

MICROPLANKTON

TERMINOLOGY AND PRESENTATION OF DATA

The term 'microplankton' is used here to describe the approximate size-limits of the organisms, plant and animal, captured in routine vertical hauls of the N 50 V. These nets were constructed as near to the specification of the $\frac{1}{2}$-m. nets previously used by the 'Discovery Investigations' as post-war materials permitted. The finest bolting-silk obtainable was found to give an approximate mesh size of $40 \times 50\,\mu$ in use. Some few large organisms are present in the catches, and have been tabulated with the others in the summarized results of numerical estimations, but general sampling of the microplankton, more especially of the phytoplankton, was the primary purpose of these hauls.

This definition of the term microplankton agrees with the usages of Sverdrup, Johnson and Fleming (1946, p. 275), based largely on that of Ekmann (1935). They relate the general terms expressive of size limits to methods of capture, thus:

*Macro*plankton: captured by coarse or medium tow-nets.

*Micro*plankton: captured by the finest grade silk nets.

*Nanno*plankton: liable to escape the finest silk, hence also 'centrifuge plankton'. Also studied by using fine filters, sedimentation methods, etc.

The nannoplankton (Lohmann) may be said to include or overlap various groupings of minute forms proposed by more recent specialist workers, such as 'μ-flagellates', 'ultra-plankton' and 'hekisto-plankton' (Cole, 1952).

Though the usage has varied we find that the outstanding plankton workers of the past agree upon the necessity of treating these generally descriptive terms in an elastic manner (cp. Steuer, 1911; Johnstone, Scott and Chadwick, 1924). At first the prefixes macro- and micro- seem to have referred broadly to large plankton organisms visible to the naked eye, and to the host of smaller forms that can be seen with the aid of the microscope. But Johnstone, Scott and Chadwick referred all net-caught plankton to the macroplankton, so that for them microplankton became synonymous with Lohmann's nannoplankton.

Meunier (1913) intended his use of the term microplankton to be construed in the earlier sense, but with restricted application: to unicellular organisms only. This would very nearly meet our needs in discussing the Benguela current material, were it not that the multicellular alga *Trichodesmium* is of some importance among the phytoplankton in that region. Moreover, the relative abundance of the smaller metazoa is obviously an important factor if the 'conditions of life' of the phytoplankton are to be considered.

More recently Ekmann (1953, p. 312), while adhering to his own early definitions (as given by

Sverdrup *et al.*) has added approximate size-limits—60–1100 μ—for the microplankton. Now since Ekmann is dealing with zooplankton this may suit his purpose well enough; but many phytoplankton organisms, especially colonial diatoms, are well sampled by nets, although the individual cells are well below 60 μ in greatest dimensions. The colonial habit permits their retention by the silk, while their highly developed powers of flotation lead to differential settling-rates or actual failure to settle, defeating the centrifuge or reversing-microscope methods of estimating relative abundance, that would otherwise be far more satisfactory than the old net method. The postulation of actual size-limits also brings us up against the fact that in Nature individual species can always be found whose normal range of size-variation bestrides any proposed limit. Many individual species of diatoms and of dinoflagellates normally vary in size from about 35 μ to over 100 μ, and a single important example of a species completely overlapping the proposed upper limit is provided by the well-known *Noctiluca miliaris*. Most samples of this cosmopolitan organism that we have examined, from many parts of the world, have had the majority of individuals ranging between 300 and 600 μ in greatest dimensions, but some frequently attain to 1200 or 1500 μ and have been known to reach 2000 μ (Lebour, 1925, p. 69). Clearly we must admit with Gran (in Murray and Hjort, 1912) and with Johnstone, Scott and Chadwick (1924, p. 75) that '. . .it is impossible to establish clear and absolutely logical distinctions. . .' in the application of these broadly classificatory terms.

. This becomes even more obvious when other technical terms, broadly descriptive of aetiological attributes of various categories of plankton organisms, such as those introduced by Haeckel and the Kiel school of planktologists, and by other workers in this field from many countries, come under review (cf. Hart, 1942, p. 268). They are but a part of the jargon without which generalizations cannot be succinctly expressed, and attempts to define them with undue regard to a rigid specialized connotation lead to frustration, because Nature herself seems able to find 'exceptions to every rule'. This obtrusive antithesis should not mean that naturalists must foreswear the ecological point of view. Major types of woodlands, whether defined by foresters or (in somewhat different terms) by terrestrial plant ecologists, are none the less real entities because some kinds of trees are to be found in more than one of them.

This problem of terminology may be partially solved by the growing practice of holding international conferences of recognized leading workers in a given subject, to seek agreement on definitions acceptable to the majority. The alternative is for the individual worker to redefine his own usage when necessary.

The first solution is hampered by language difficulties and the rank growth of 'the literature', such that the richest of languages proves insufficient to provide suitable terms that can be used in specialized connotation, without trespass upon the jargon of some other 'branch of knowledge'. The second, to some extent inescapable, can easily lead one into tedious and unprofitable etymological discussion!

Here we attempt a working compromise by following the usage of Sverdrup, Johnson and Fleming (1946) for most ecological terms. This usage is mainly derived from that of the earlier works mentioned above. When less widely known terms have been employed we have tried to make their meaning plain from the context where they first appear. The meaning of some phrases coined merely for description of the present data will, we hope, prove sufficiently clear if the words are read in their generally accepted, non-specialized sense.

Terms relating more particularly to the phytoplankton are used in the sense that Gran and Braarud (1935) have ascribed to them, as nearly as the differing conditions in this part of the southern hemisphere permit. They have been evolved from the earlier system of 'plankton elements' devised by Gran (1902, 1932) for ecological characterization of the species, during the period when plankton

workers were gradually building up concepts capable of wider application than the older 'plankton types' of Cleve.[1]

Gran's system itself involves the use of some of Haeckel's terminology. 'Holoplanktonic', 'meroplanktonic' and 'tychopelagic', defining the degree to which organisms are dependent on the sea bottom at some period of their history, are widely accepted. 'Oceanic' and 'neritic', however, can soon lead to anachronisms in dealing with the phytoplankton, if applied in a rigidly restricted sense (cf. Hart, 1942, p. 283). Many undoubtedly holoplanktonic 'oceanic' diatoms, to be found in the open sea at all seasons, may attain considerable abundance in coastal ('neritic') sea-areas. Conversely many 'meroplanktonic' (and therefore truly 'neritic') species seem able to go on reproducing vegetatively for so long that they may often form a considerable proportion of the phytoplankton in some 'oceanic' areas far beyond the edge of the shelf.

To avoid the confusion that could arise through the necessity of listing some species as both oceanic and neritic, we suggest the use of the word 'panthalassic' to describe these ubiquitous forms. The word was used by Johnstone, Scott and Chadwick (1924) and is given in *Henderson's Dictionary of Scientific Terms* (1953) as: 'living both in coastal and offshore waters; neritic and oceanic', but we have not yet discovered who first used it in this sense.

To distinguish species of very wide distribution, whether neritic, oceanic or panthalassic, we have here used the adjective 'cosmopolitan' in its general sense, when their known distribution shows a higher degree of tolerance towards temperature and salinity differences than is *necessarily* shown by all the panthalassic species. There are many regions where occupation of both inshore and offshore waters does not involve very wide tolerance of these two best-known parameters of the surface-waters.

Use of the expressions 'dominant' or 'predominant', practically unavoidable in discussing differences between phytoplankton populations, provides another example of the difficulties involved when words so useful in their generally accepted sense acquire an arbitrary, specialized connotation, through the attempt to define them objectively. Numerical preponderance at some arbitrarily chosen level can be misleading (from the point of view of potential productivity) of organisms varying so widely in size and shape, and invites the further criticism that all known counting methods involve errors. Yet, if we are to attempt anything less subjective than the addition of such descriptions as 'abundant', 'common', or 'rare' to the organisms identified, some form of counting—and acceptence of arbitrary levels in drawing deductions from the counts—is unavoidable. Conversely, it should not be forgotten that *admittedly* subjective observations by the earlier naturalists lead to the first recognition of any recurring pattern of plankton distribution.

The whole subject is one to raise echoes of the resounding controversies, as to methods of quantitative plankton investigations, that followed publication of Haeckel's famous *Plankton Studien*, and the replies of Hensen and others, of which the best brief account that we have come across is given by Johnstone (1908).

Throughout the subsequent development of plankton study the early methods have been periodically subjected to destructive criticism, too often by those who have never learnt to count plankton, and constructive reviews like that of Gran (1932) have been few. Considerations which should help to place the matter more fairly in perspective are:

First, the truism that the ideal comprehensive quantitative method may indeed be approached, but

[1] Cleve's 'Plankton Types' constitute the first clear epitome of the close relation between plankton population and conditions of the *milieu*, that may be evident whenever neighbouring water masses are exceptionally well defined. When further work made it clear that water-movements and seasonal changes frequently produced more complicated inter-relationships, it was against the background of Cleve's concept that the new evidence was marshalled. Cleve's 'types' are still distinguishable in essence wherever abrupt differences in environment recur with the consistency usual around southern Scandinavia, but few sea-areas provide such clear-cut examples.

never achieved. Hensen himself had discovered that methods had to be varied to suit the study of different organisms.

Secondly, the necessity for wide, rapid coverage in collection, especially in the less known areas. This often renders crude estimates of relative frequency of greater immediate value than limited series of more accurate data, and was the main reason for our choice of an 'antiquated' method here. The principle is epitomized in Gran's phrase 'a single "absolute" estimation of phytoplankton would be about as valuable as a single temperature determination carried to the third decimal place'.

We have used Hensen's methods for subsampling and counting from routine vertical hauls of the fine silk $\frac{1}{2}$-m. net (N 50 V), but do not follow the early workers in regarding the hauls as representing a constant fraction of the entire contents of the theoretical volume of water filtered. The estimations from counts we regard as roughly comparable indications of relative abundance, within the limits of the very large differences involved in plotting (say) the estimated totals on a logarithmic scale. They are, however, much more accurate as regards the relative importance of species within single samples; and more accurate for small samples than for large ones that have to be diluted to render subsamples small enough to count.

We have found it easier to appreciate the relative frequencies involved by tabulating the actual estimated numbers in primary tables, but in any form of graphic representation it becomes necessary to use logarithmic or other functional ordinates. For the logarithmic reductions we have the classic precedent of Professor Hentschel's work on the 'Meteor' centrifuge-plankton (Hentschel (1936)), and the wide applications of logarithmic scales in dealing with many types of biological data have more recently been well reviewed by Williams (1947). Other scale reductions are indicated on individual diagrams, and it is hoped that sufficient tabular data are included to forestall queries arising from the distortions unavoidable in graphic presentations of this kind.

Recognizing the limitations of these numerical estimates, derived from roughly comparable hauls, the necessity to adopt some arbitrary definition of dominance must still be faced; though we have ventured to retain such useful expressions as 'frequent' and 'important' in their loose, generally accepted sense. Now, the surveys were planned to include observations within two distinct types of surface-water and the boundary region between them. Hence our criterion of dominance must be applicable to individual samples. We cannot, for instance, employ some method like that of Sargent and Walker (1948), who determined most satisfactory levels of significance (on a percentage basis) by pooling results from a whole series of observations. Their method, one of the best we have yet seen, demands, first, that the observations be restricted to a single water mass (though 'succession' with increase in 'age' of the surface-water may be apparent), and, secondly, adequate seasonal coverage; so that 'succession' should not be confused with 'sequence' (i.e. changes in population due to invasion of the area by a different water mass).

Our definition derives direct from the raw data—the estimates of numbers of each category recognized (some 12–50 categories) at each of the eighty-odd stations, arrayed in numerical order from the original counts. We regard the first seven on each list as 'dominant'. By this means the local importance of the more exclusively offshore species is not obliterated by the vast preponderance of the inshore forms, as it would be if the results from the whole of this survey area were pooled. Further, the local importance of some panthalassic species, present in the proportion of (say) 20,000/100,000 at some impoverished offshore station, is not obscured by its presence in greater quantity—perhaps 200,000—at a rich inshore station where the estimated total might be some 200 million, and the first eight or ten categories all exceed two million.

Considering only the thirty-nine stations from each survey that were repeated at approximately the

same positions,[1] this arbitrary choice of a level of 'dominance' was found to show the following results:

(a) The lowest (7th) 'dominant' ranged between 0·7 and 7·1% of the estimated total, *mean 3·5%* with σM 1·3. At only two of the seventy-eight stations was its value below 1%, and although the 5% level was exceeded at 8/78 stations, the eighth number of the list (highest category excluded on this scheme) exceeded 5% of the total once only.

(b) The sum of the 'dominants', i.e. $\sum_{7th}^{1st}$ of the numbers on each list, ranged between 59·8 and 99·6% of the estimated totals, *mean 81·6%* with σM 10. The level fell below 60% at one station only, below 65% at 5/78 stations, and it exceeded 95% at 6/78 stations.

For the four samples of visibly discoloured surface-water, three examined by the drop method and one with the aid of the centrifuge, the 5% level was chosen as the lower limit of 'dominance'.

In the primary tables for the first (autumn) survey the stations numbers are given in chronological order as they were worked, from north to south. During the second survey interpolation of extra stations (mostly for bottom-sampling) and the fact that it was worked from south to north destroys the sequence of the serial numbers. The data have, therefore, been listed so that microplankton data from repeat positions are given in the order in which the corresponding stations had been occupied during the first survey. Although this results in the last becoming first, it should not be confusing because, if the serial numbers are disregarded, it also has the result that observations made in equivalent positions are treated in the same sequence in the Tables for each survey (cf. Figs. 1 and 2, and Tables 14 and 15).

Stations where full series of hydrological and plankton observations were made have been distinguished by printing their serial numbers in ordinary type, while those where only the microplankton net and bathythermograph were used are given in italics.

As an aid to verbal description, the four main lines of observations worked east and west have been named from the most prominent topographical features near their coastal terminations, in order from north to south: the Möwe Point line, Walvis Bay line, Sylvia Hill line and Orange river line. The three lines of subsidiary observations connecting them have been termed the northern, mid- and southern intermediate lines. Approximate mean latitudes for stations worked on each of the four main lines are: Möwe Point line, 19° 40′ S.; Walvis Bay line, 22° 40′ S.; Sylvia Hill line, 25° 20′ S.; and the Orange river line 28° 40′ S.

The order in which groups of organisms, and lesser taxonomic units within the groups, have been arrayed in tables and diagrams, has been governed by the main object of this part of our work: description of the rich microplankton flora as a whole. Strict adherence to the sequence of some recognized scheme of classification would render them very cumbersome and even perhaps misleading, owing to the impracticability of publishing the raw data in full, or of identifying members of all groups down to the same taxonomic level. These difficulties, added to the admittedly unequal sampling of certain groups by the net method, have prompted the following explanation of the relation between our arbitrary arrays and systematic classification, since we have no wish to do violence to systematists' views, whenever they seem well established.

First we give the sequence of main groupings represented in the Benguela current samples, all of which, excepting the silicoflagellata,[2] are usually regarded as classes of algae, according to the classification of Fritsch (1935, 1945)—perhaps the most widely accepted at the present time.

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[1] That is omitting the extra stations worked south and north of the main survey area during the second survey.

[2] Fritsch treats the silicoflagellata, whose affinities are still in doubt, as a minor group of uncertain status, at the end of his discussion of the chrysophyceae. We are indebted to Dr M. W. Parke of the M.B.A. Laboratory, Plymouth, for advice on this point.

The five classes out of the eleven considered by Professor Fritsch that were not represented in our material have been omitted. They include the large thallose, attached marine forms, and others with few, if any marine representatives. The sequence of his scheme is indicated by the roman numerals. To each group a summary of the disposition of individual categories (whether species, genera or larger units) that we recorded, has been added:

I CHLOROPHYCEAE. With two species of *Trochischia*, rarely and in small numbers only.

II XANTHOPHYCEAE. *Halosphaera* only, extremely local.

III CHRYSOPHYCEAE. With the Coccosphaeriales lumped here because they cannot be adequately sampled by nets (numerically they are a most important group in warmer seas, as nannoplankton methods have shown). *Phaeocystis*, here mercifully less abundant than in colder seas.

Silicoflagellata. With two species, never very abundant but widely distributed.

IV BACILLARIOPHYCEAE. With ninety-five species or generic categories.

VI DINOPHYCEAE. With forty-two categories, although only the *Ceratia* and a few most obviously important of the other thecate forms were identified down to species.

XI CYANOPHYCEAE. Only one important species here: *Trichodesmium thiebautii*.

From the 'Meteor' results (Hentschel, 1936) we know that the Coccosphaeriales, smaller Dinophyceae and even some of the Chlorophyceae, would figure much more prominently in relation to members of the other groups, if we were considering 'ideal' samples in which nanno- and microplankton forms were represented with equal fairness. On the other hand, *Halosphaera* and the silicoflagellates belong to groups wherein few marine species are known, whatever method of collection is adopted. These limitations, especially those implicit in the choice of the net method, our reasons for which have already been mentioned, led to the decision to treat the phytoplankton under three main headings: Diatoms (Bacillariophyceae), Dinophyceae and 'other Protophyta' or 'other plants'; that is, in descending order of their abundance in these samples, in our main list and primary tables and diagrams.

Within these groups the order of genera adheres to recent systematic practice, though the more detailed description of the diatom flora has involved some arbitrary arrays to be described later.

In the main list the genera of diatoms follow the classification proposed by Hendey (1937), but the species within each genus are arranged alphabetically, because the subgeneric arrangements proposed for some large and important genera are still highly debatable. The Dinophyceae follow the sequence used by Schiller (1933), and the heterogeneous assemblage of 'other plants' the order in which their main groups occur in Fritsch's general classification of the algae.

Chief among the many works consulted for identifications were the Nordisches Plankton series and, for the diatoms, Lebour (1930), Hustedt (1927–37), Hendey (1937) and Boden (1950). For the Dinophyceae, Lebour (1925) and Schiller (1933) were of the greatest assistance.

The Protozoa and Metazoa have been treated less thoroughly than the phytoplankton in these samples because the larger ones were better sampled by coarser nets. The genera of Tintinnoinea were determined with the aid of Kofoid and Campbell's Monograph (1929), but to have done the same for the Radiolaria (equally important at a few stations) was beyond my capacity (T.J.H). Similarly, among the Metazoa, while some individual species of local importance were recorded separately, the Nauplii and other larval categories are quite unequal in systematic status. These diverse groups of animals are listed as nearly to the generally accepted taxonomic order as their nature permits.

The diatoms being by far the most abundant organisms in these samples, are discussed in greater detail than the other main groups, and hence we endeavour to make plain the inter-relations between systematic classification, and arbitrary arrays used merely as an aid to presentation of data, at the outset.

Hendey's classification of the class Bacillariophyceae (diatoms) aims at providing a system wherein the great structural differences between the most abundant plankton forms are more clearly emphasized than they were in earlier systems; among which that of Schütt (1896) with minor modifications by subsequent workers, is still the most widely accepted arrangement.

Schütt's scheme divided the whole group into two suborders Centricae and Pennatae, based upon cell-symmetry around a supposedly central point in the one group, and a more or less iso-bilateral symmetry in the other. Most marine plankton forms belong to the Centricae; and the majority of the attached marine forms, freshwater and soil diatoms to the Pennatae. To this extent the scheme shows a reflection of the earlier ideal, ultimately found impracticable, of classifying diatoms principally upon the mode of life, as Smith (1853–6) had tried to do. The main morphological basis of Schütt's scheme soon shows up the incompatibility: although most of his Pennatae are not to be found as normal constituents of the marine phytoplankton, some lesser subdivisions of the group are well represented therein; so that the agreement between systematic classification based on morphology and primary habitat differences, although better than it is in many other classes of organisms, is by no means complete.

Hendey (1937, 1951) has pointed out that the major subdivisions of the Centricae (variously ranked as sections, families or tribes in later modifications of Schütt's scheme) show structural differences so marked that their inclusion within a single suborder seems questionable. Some of them (Biddulphineae, Soleniineae) even show a type of symmetry that it is very difficult to relate to a supposedly central point. Moreover, even the Pennatae include groups of very diverse structure, although they do not show such extreme divergence from the main characters of the suborder as do some of the Centricae.

Hendey, therefore, proposed that the class Bacillariophyceae, regarded as including only the one order Bacillariales, should be divided into ten suborders of equal systematic status. The first five of these include the forms assigned to various minor rankings in the more recent modifications of Schütt's Centricae (e.g. Hustedt, 1927–37) while the last five were included in Schütt's Pennatae. Hendey (1937) has himself pointed out that with regard to rankings below the level of suborders, his arrangement is not materially different from the earlier ones, and he has been at pains to make due acknowledgement to Schütt and other workers in this field. The formal terminations of the family and subfamily names that he has adopted merely serve to render his classification of the Bacillariophyceae consistent with generally accepted usage among other classes of algae.

Table 11 shows Hendey's classification, excluding the genera not represented in the material that he was working on when he first formulated it. That material consisted of a large selection of plankton samples from most of the areas traversed by ships of the Discovery Investigations in the Southern Hemisphere, prior to 1935.

In Table 11 the genera and corresponding supra-generic rankings observed in our Benguela current material have been printed in ordinary type, leaving the groups that have as yet been recorded only from other parts of southern seas distinguished by italics.

Supra-generic rankings, either at the level of suborder or family, were found to lend themselves to the definition of four of the five arbitrary groupings used later in this report, for descriptive purposes only. They are preceded by numbers in brackets, and printed in bold type in Table 11.

The fifth group is a lumping of such members of the last five of Hendey's suborders as occurred in the Benguela current samples. In this report they have been termed 'Pennatae' for the sake of brevity *not* from any desire to revert to the older classification.

Whether one thinks of them as the Pennatae of Schütt, or the last five suborders of Hendey's system, those familiar with marine phytoplankton will know that nearly all the planktonic members

Table 11. *Classification of plankton diatoms proposed by Hendey (1937) with the genera and higher groups seen in the Benguela current material in ordinary type, others in italics. Note: this is not a complete classification, many non-marine or non-planktonic genera having been omitted. Inclusion of all diatom genera would slightly alter the sequence of some of the units of less than sub-ordinal rank.*

The first four of the five arbitrary groupings used for descriptive summaries in this report coincide with suborders or families in the system, and are shown below in heavy type. The fifth group, a heterogeneous lumping from the last five suborders, has been termed 'pennatae' for the sake of brevity, but is not intended to imply reversion to earlier classification (see text)

Sub-orders	Families	Sub-families	Genera
DISCINEAE			
	Coscinodiscaceae		
		Melosiroideae	
			Melosira
			Hyalodiscus
		Skeletonemoideae	
			Skeletonema
			Stephanopyxis
			Detonula
		Thalassiosiroideae	
			Thalassiosira
			Coscinosira
			Lauderia
			Schröderella
			Bacterosira
		Coscinodiscoideae	
			Coscinodiscus
			Charcotia
			Planktoniella
			Gossleriella
			Schimperiella
			Actinocyclus
	Hemidiscaceae		
		Hemidiscoideae	
			Hemidiscus
	Actinodiscaceae		
		Stictodiscoideae	
			Stictodiscus
			Arachnoidiscus
		Actinoptychoideae	
			Actinoptychus
		Asterolamproideae	
			Asterolampra
			Asteromphalus
AULACODISCINEAE			
	Eupodiscaceae		
		Pyrgodiscoideae	
			Pyrgodiscus
		Aulacodiscoideae	
			Aulacodiscus
		Eupodiscoideae	
			Eupodiscus
AULISCINEAE			
	Auliscaceae		
		Auliscoideae	
			Auliscus
BIDDULPHIINEAE			
	Biddulphiaceae		
		Biddulphioideae	
			Biddulphia
			Bellerochea
			Cerataulus
			Cerataulina
		Triceratioideae	
			Triceratium
			Trigonium
			Pseudotriceratium
			Lithodesmium
			Ditylum
		Hemiauloideae	
			Hemiaulus
		Eucamphioideae	
			Eucampia
			Streptotheca
			Climacodium
	Anaulaceae		
		Anauloideae	
			Anaulus
	Chaetoceraceae		
		Chaetoceroideae	
			Chaetoceros
SOLENIINEAE			
	Bacteriastraceae		
		Bacteriastroideae	
			Bacteriastrum
	Rhizosoleniaceae		
		Rhizosolenioideae	
			Rhizosolenia
			Guinardia
	Leptocylindraceae		
		Leptocylindroideae	
			Dactyliosolen
			Leptocylindrus
	Corethronaceae		
		Corethronoideae	
			Corethron
ARAPHIDINEAE			
	Fragilariaceae		
		Fragilarioideae	
			Fragilaria
			Fragilariopsis
			Asterionella
			Synedra
			Thalassionema
			Thalassiothrix
		Meridionoideae	
			Meridion
		Tabellarioideae	
			Licmophora
			Grammatophora
			Striatella
			Rhabdonema
			Entopyla
RAPHIDIOIDINEAE			
	Eunotiaceae		
			Eunotia
MONORAPHIDINEAE			
	Achnanthaceae		
		Achnanthoideae	
			Achnanthes
		Cocconeioideae	
			Cocconeis
BIRAPHIDINEAE			
	Naviculaceae		
		Naviculoideae	
			Navicula
			Trachyneis
			Scoresbya
			Pleurosigma
		Amphiproroideae	
			Amphiprora
			Tropidoneis
	Gomphonemaceae		
		Gomphonemoideae	
			Gomphonema
	Cymbellaceae		
		Cymbelloideae	
			Cymbella
			Amphora
	Epithemiaceae		
		Epithemioideae	
			Epithemia
	Bacillariaceae		
		Nitzschioideae	
			Nitzschia
			Chuniella
		Bacillarioideae	
			Bacillaria
SURIRELLINEAE			
	Surirellaceae		
		Surirelloideae	
			Surirella
		Campylodiscoideae	
			Campylodiscus

of this group belong to the two families Fragilariaceae and Naviculaceae, with a few species of the genus *Nitzschia*. These forms, which fall into the suborders Araphidineae and Biraphidineae of Hendey's system, exhibit features that fit them for a free-floating existence (if the teleological expression may be forgiven). Such features are the development of catenary, branching or ribbon-forming colonies; attenuated form of the individual cells; or the possession of cell-walls much slighter than those of their bottom-dwelling relatives. Indeed, in an aetiological sense, they have collectively been well described as 'reversionary plankton forms', by Lloyd (1926). However, in this material, as in that from other coastal areas, we find that a small proportion of bottom-dwelling forms (e.g. *Achnanthes* which falls within Hendey's Monoraphidineae) occur tychopelagically in the plankton. In need of a summary group-heading that would include these also, it was felt that the old term 'Pennatae', though of doubtful value in its taxonomic sense, would be more convenient than some cumbersome phrase such as 'last five suborders'. The expression 'small pennate diatoms' that Marshall (1933) found convenient for ecological description of material from the Great Barrier Reef, is only a partial equivalent, since large species like *Thalassiothrix longissima* and *Pleurosigma capense* are included in the Benguela grouping.

For the rest, Hendey's suborder Discineae suited our purpose well as it stands, but coming to the suborder Biddulphineae it seemed best to divide the outstandingly abundant Chaetocerids from the others at family level, for the latter derive from several subfamilies, whereas the Chaetoceraceae include but the one subfamily, and indeed, in this material, only the one genus. The Soleniineae, consisting almost exclusively of holoplanktonic forms, provided a convenient grouping at the level of the suborder.

Thus four of our five arbitrary groupings can be defined in terms of widely accepted systematic assemblages, though these are not of equal status. The fifth group remains heterogeneous. Abstracting them from the classification table, and summarizing their main ecological characteristics, we have:

I Suborder **Discineae**. Most of the species neritic and probably meroplanktonic, with heavily silicified frustules. Exceptions (holoplanktonic, relatively more abundant in the sparser phytoplankton at greater distances from land) were *some* of the *Thalassiosira* spp. and the definitely oceanic *Planktoniella*. The colonial habit and gelatinous or spiny projections of the former, and thin, hyaline, ribbed extensions of the valve margins of the latter, may conceivably assist flotation.

II Family **Biddulphiaceae**. Mainly neritic, few solitary, but the others showing very varied development of the colonial habit. A few are oceanic, holoplanktonic (very rare in these samples, e.g. *Hemiaulus Hauckii*). Majority meroplanktonic (*Eucampia*, *Biddulphia*) or even bottom-dwelling species (*Triceratium*) whose occasional presence alive in the plankton may justify their inclusion as tychopelagic species.

III Family **Chaetoceraceae**. Mainly holoplanktonic in the vegetative phases, but a majority form specialized resting spores and are, therefore, probably meroplanktonic. Many neritic, few oceanic species. In comparison with II, with which they form the suborder Biddulphiineae, the Chaetoceraceae show an increased development of structural features that must tend to aid flotation: thin, less strongly silicified frustules, and horns produced into long setae. Mainly colonial.

IV Suborder **Soleniineae**. Nearly all holoplanktonic, many oceanic or panthalassic, few neritic. Structurally they include large and medium-sized tubular species, solitary or in colonies of few cells and long chains of small cylindrical species.

V '**Pennatae**'. A heterogeneous arbitrary grouping, as explained in detail above. It consists of the few normally planktonic members of Hendey's Araphidineae and Biraphidineae (the 'reversionary plankton forms' of Lloyd) with such few bottom-dwelling forms from the last five of Hendey's sub-

orders (Pennatae proper, if one prefers Schütt's system) as were found to occur tychopelagically in these samples. Mainly meroplanktonic, neritic.

Taxonomic notes

Changes in nomenclature of phytoplankton species have been adopted where recent taxonomic research seems to justify them. Most of these are better known to plankton workers under earlier names current in general handbooks such as Engler and Prantl's *Pflanzenfamilien*, the Nordisches Plankton series and M. V. Lebour's *Planktonic Diatoms of Northern Seas*. It is hoped that these notes may prevent further confusion. They give first the name used in this report in bold type, the best known previous synonym, and then the authority for the change. *Full* synonymy is *not* attempted here. Some brief comment has been offered concerning changes that still seem to the writer to be of doubtful value, but detailed taxonomic study would require a separate report. (Where the first person has been used in this section the opinions expressed are those held by one of us (T. J. H.) personally.)

Hemidiscus cuneiformis Wallich (1860), formerly *Euodia cuneiformis* (Wallich) or *E. cuneiformis* Schütt.

Hustedt (1927–37, p. 903) and Hendey (1937, p. 264) have explained how the foundation of several species that they believe to be but varieties or phases of the type, coupled with Castracane's error in supposing that *Euodia* Bailey, 1861, predated Wallich's foundation of the genus *Hemidiscus*, has led to prolonged uncertainty as to the correct naming of this species. It is interesting to note that in all the welter of confusion Cleve (1901, p. 330) had worked back to the combination now considered correct, although he later supported Gran's use of *Euodia cuneiformis* (Wallich) as synonymous with *E. gibba* Bailey (Gran, 1905, p. 45).

Actinoptychus senarius Ehrenberg, previously widely known as *A. undulatus* (Bailey). Hendey (1937, pp. 271–2) shows that Ehrenberg's specific name should be adopted upon grounds of priority. Confusion arose because Ehrenberg first described it as a species of *Actinocyclus* (Ehrenberg, 1838). Later he himself recognized the structural differences that seemed to warrant the splitting of this genus into *Actinocyclus* as most subsequent workers have known it, and *Actinoptychus* which he established as a distinct genus, with *A. senarius* as the type-species (Ehrenberg, 1841, 1843). The figures of this form given as an unnamed species of *Actinocyclus* by Bailey (1842) first received the specific epithet *undulatus* from Kützing (1844), and the combination *Actinoptychus undulatus* (Bailey) was made by Ralfs in the fourth edition of Pritchard's *History of the Infusoria*, 1861! Ehrenberg himself seems to have had no doubt that the unnamed figure of *Actinocyclus* sp. given by Bailey, and later called *Actinocyclus undulatus* by Kützing, was specifically indentical with his own '*Actinocyclus*' (later *Actinoptychus*) *senarius* (Ehrenberg, 1843, p. 328).

Cerataulina pelagica (Cleve) Hendey comb. nov., more widely known as *C. Bergonii* H. Peragallo or *Cerataulus (Cerataulina) Bergonii* (H. Peragallo).

Hendey (1937, p. 279) states that though Peragallo first suggested the need for a new genus (*Cerataulina*) when he described the species *Cerataulus (Cerataulina) Bergonii* H. Peragallo (1892), he did not define that genus. Later it appears that Cleve (1894, p. 11) accepted Peragallo's tentatively proposed name, while pointing out that the form which he had himself described earlier as *Zygoceros pelagicum* (Cleve, 1889, p. 54) was a complete synonym. Yet the genus *Cerataulina* does not seem to have been properly established anywhere until Schütt's publication of 1896 (in Engler and Prantl, p. 95). Hendey's proposed combination seems the only means of bringing the species within the bounds of accepted rules of nomenclature, though plankton workers have been familiar with '*C. Bergonii*' for so long that they cannot but regret the change.

Chaetoceros atlanticum var. (or phase) neapolitana (Schröder) Hustedt, previously often re-garded as a distinct species, *C. neapolitana* Schröder. Here lumped with the type.

Gran and Yendo (1914) noted that this form, which they regarded as a distinct species, was most often to be found in the warmer waters around Japan, while the highly variable and cosmopolitan *C. atlanticum* Cleve was mainly confined to the colder water masses in that region. Earlier work round Japan suggests that the *neapolitana* form might be found in the colder waters also. Though Okamura (1907) identified his specimens as *C. atlanticum*, Gran and Yendo seem satisfied that they were the *neapolitana* form, and doubted the localities whence they were recorded in consequence!

Hustedt (1927–37), Hendey (1937) and Boden (1950), the latter working on South African material, have regarded *neapolitana* as a variety of *C. atlanticum*. It was Hustedt who regularized this change, and both he and Hendey also dealt with the very confused synonymy of the type.

Our material seems clearly to support the view that *neapolitana* can hardly be a separate species. Both the type (*C. atlanticum*) and the variety occurred together at some stations near the shelf-edge, with seemingly intermediate forms, and *neapolitana* more frequently than type or intermediates in the warmer oceanic water still farther offshore.

The regular banded appearance of the setae, due to chloroplasts penetrating into them and disposed at regular intervals, was very characteristic of the *neapolitana* phase, and is shown in figures of material from other localities by Schröder himself (1900) and Cupp (1943) among others. However, our material also showed individual colonies of both type and intermediates with a similar disposition of chloroplasts. We have to remember that the movements of chloroplasts within the shell are probably governed by light intensity. Hence this appearance in preserved samples may depend more upon the depth at which they were captured and time interval prior to fixation than upon any greater tendency towards this pattern in the *neapolitanum* phase, rather than in type or 'intermediate' strains.

Certainly we would agree with Gran and Yendo that *neapolitana* is a warm-water phase of the species, and this is also the view of Cupp (1943) and Takano (1954) who gives excellent figures of what he terms var. *neapolitana* and var. *skeleton*.

It seems significant to me that when material from the north-eastern Atlantic only has been studied, there are many examples of diatoms that show a polymorphism, seemingly so definitely related to temperatures (and therefore having a distinctive space/time distribution) that systematists have failed to agree upon the specific or subspecific status of the different forms. Yet, when material from regions with steeper temperature gradients has been examined, these same cosmopolitan diatoms have seemed to fall much more convincingly into categories of less than specific rank (often obviously linked by intermediate forms) of single types. Thus these chaetocerids, and the solenoids mentioned below, seem justifiably 'lumped' on the basis of our Benguela current material, derived from a typical upwelling region where the temperature gradients are frequently very steep. Such abrupt variations in temperature are also to be found near the northern limits of the Kuroshiwo current, whence some of Gran and Yendo's material and most of Takano's was derived.

Chaetoceros costatum Pavillard, previously widely referred to as *C. adhaerens* Mangin.

This change was advocated by Hustedt (1927–37, pp. 699–700). Its propriety is not very obvious from the figures he reproduced from Pavillard and from Mangin. Cupp (1943, p. 127) follows Hustedt and gives better figures, that agree well with the varied South-west African samples we studied.

In our material the species was very restricted in distribution, but abundant at four autumn stations inshore. Here the range of variation in dimensions coupled with the presence of mucous (or 'pecti-naceous') cushions between corners of adjoining cells, a character of Mangin's definition, in chains that also displayed the intercalary bands shown by Pavillard's figure, led me to conclude that Hustedt

is correct in accepting Pavillard's specific name on grounds of priority (Pavillard, 1911, p. 24, fig. 1 *b*, *c*; Mangin, 1912, p. 39, fig. 25, pl. II, fig. 10).

The intercalary bands arranged in imbricating fashion were hard to see in some of the colonies, and many of the frustules resemble the two lower ones in Pavillard's figure, where the bands are visible only where they approach the cell margin as seen in broad girdle view. Such banding on the connective zone is a rare feature among Chaetocerids, viewed under ordinary conditions, but characteristic of the related genus *Attheya*.[1]

Some of our material even suggested that *Chaetoceros imbricatus* Mangin (1912, fig. 37) should also perhaps be considered as a synonym of *C. costatum* Pavillard, the cells in the chains were so closely adpressed, but I could not feel sure of distinguishing between these forms and phases of *C. didymum* like the var. *agregata* also figured by Mangin (1912, fig. 37) from the type locality of his *C. imbricatus* off Brest, under the working conditions imposed by normal plankton analysis. *C. didymum* was exceedingly abundant, in a welter of varieties or phases, at most inshore stations during our Benguela current survey. The question must be left open, with the admission that further detailed work may serve to show the presence of *C. imbricatus* Mangin here, and that it may have been wrongly included with *C. costatum* Pavillard, or with some phase of *C. didymum* in my counts. As the numbers involved were exceedingly small in comparison with those of clearly indentifiable species, the point is of small moment in considering the diatom flora as a whole.

Chaetoceros subsecundum (Grunow) Hustedt formerly known as *Chaetoceros diadema* (Ehrb.) Gran.

Hustedt (1927–37, p. 645) details the argument by which, under the International Rules for Botanical Nomenclature, the widely known specific name *diadema*, finely descriptive of the resting spores, and based on *Syndendrium diadema* Ehrenberg 1854, should be supplanted by the above combination, based on *C. distans* (Cleve) var. *subsecunda* Grunow (ex Van Heurck, 1881 (1880–5).

It appears that Grunow was right to reject *diadema* on realizing that the forms in question were related to *Chaetoceros*, *Syndendrium diadema* becoming a *nomen confusem*, since it was based upon the resting spores only. Unfortunately, Grunow was mistaken in relating it to *C. distans* Cleve (1873), itself a misidentification of *C. dichaeta* Ehrenberg. It thus became necessary to elevate the varietal name to specific rank as Hustedt has done, though there is still much doubt and confusion about the full synonymy.

I am greatly indebted to Mr N. I. Hendey for a personal communication helping to clear up this obscurity.

Rhizosolenia imbricata Brightwell var. (or phase) **Shrubsolei Cleve**, often previously considered as a distinct species, *R. shrubsolei* Cleve.

Our Benguela material of this usually small and narrow form of comparatively cold waters seems to me to provide ample support for the view that it is not specifically distinguishable from the stouter form of warmer seas described as *R. imbricata* by Brightwell.

Hustedt (1927–37, p. 584) gives formal expression to this view, and points to the synonymy with *R. striata* Greville and the apparent lack of justification for the establishment of Peragallo's *R. atlantica* and *R. pacifica*, both seemingly also synonyms of *R. imbricata* Brightwell.

A footnote of Gran's (1905, p. 52) anticipates Hustedt's decision, pointing out that if the specific identity of the two forms could be demonstrated, Brightwell's name should be the one used on priority grounds, and it would seem that Cleve himself had drawn attention to the matter.

At several Benguela current stations both forms were present, mainly very much as figured by Lebour (1930, p. 97) under the name *R. shrubsolei* Cleve, but many individuals intermediate both with

[1] Intercalary bands have also been described in *Chaetoceros teres*, visible only after special treatment and mounting (Mangin, 1908) and in *Chaetoceros eibenii* by Pavillard (1921).

regard to their size and degree of flattening of the valves were also present. Also I gained a distinct impression of a relative increase in numbers of the stouter form in the warmer waters *before* re-reading the debatable taxonomic literature.

Boden (1950) who worked on material from the Atlantic side of Cape Peninsula has also accepted Hustedt's view, but a full study of the earlier synonymy and detailed re-examination of our material in further support thereof would require a separate publication.

Fragilaria Karsteni Boden *nom. nov.* instead of *F. capensis* Karsten.

Boden (1950, p. 406) has explained that Karsten's term was preoccupied by *F. capensis* Grunow, 1863, which differs structurally and in size from the species under discussion, hence the need for the new name that Boden has established.

Thalassionema nitzschioides (Grunow) Hustedt, previously very widely known as *Thalassiothrix nitzschioides* Grun., Van Heurck.

Hendey (1937, p. 336) points out that although Grunow wrote of the possibility of a need to establish a new genus *Thalassionema* he did not define this proposed genus at all, and that Hustedt (1927–37, p. 244) was the first to do so. Hendey holds, therefore, that the authority should be ascribed to Hustedt.

Noctiluca miliaris Suriray, instead of *N. scintillans* (Macartney) to which this widely known organism is often referred.

On this vexed question we have accepted Schillers (1933–7) verdict in favour of the later *N. miliaris* Suriray (1816), 1836, against the earlier synonyms *Medusa marina* Slabber (1771) 1778, and *Medusa scintillans* Macartney, 1810. Kofoid (1919) who first produced good evidence of the dinoflagellate affinities of this enigmatic, heterotrophic form, preferred Macartney's specific name for it. Before that most marine biologists had used *Noctiluca miliaris* Suriray.

We have not been able to consult all the early references quoted by Schiller, but if the genus *Noctiluca* of Suriray is accepted, as it has been by almost all naturalists ever since Ehrenberg used it in 1834, it seems only consistent to use his specific name for the type-species also; since the earlier synonyms placed the organism in a 'false genus'. Under admittedly much more recent interpretations of the 'rules of nomenclature', they should therefore lapse; unless Suriray had himself decided to use one or the other in making a 'new Combination'. Most probably he did not know of the earlier descriptions.

Dinophysis tripos Gourret, previously widely known as *Dinophysis homunculus* var. *tripos* (Gourret).

It is now generally held that Stein's *D. homunculus* is a synonym, in part, of at least three of the species in the Caudata group of *Dinophysis: D. caudata* Kent, which should replace *homunculus* as a specific and as group-name on grounds of priority, *D. diegensis* Kofoid and *D. tripos* Gourret. Lebour (1925) has pointed out that in *D. tripos* the hypotheca always shows a second smaller more dorsal point, in addition to the well-defined 'Tail'; whereas in *D. caudata* varieties the tendency to form a definite projection in the corresponding position is much less pronounced. A single figure of an extreme variety of *D. caudata* from the Persian Gulf by Dr V. Pietschmann, reproduced by Schiller (1933, p. 157, f. 145, u.) shows a definite secondary 'point', but it is appreciably smaller and less acute than that of *D. tripos*, even when comparing it with the figures of the latter (several are given by Schiller) in which the feature is least developed. 'Discovery' material both from the east and west coasts of Africa seemed to me (T. J. H.) to be clearly ascribable to *D. tripos* Gourret, although *D. caudata* Kent may also be found at some of the localities.

In the Benguela current, *D. tripos* was limited to the extreme north of the area covered by our survey, and to the extra stations south of the area that preceded the second survey. It was not observed in the central portion of the coastal current where the heaviest diatom catches were taken and where

the negative temperature anomaly was greatest. This can scarcely be due to the effect of temperature, however, for the species is often abundant in water as cold as this (in the absolute sense, not in terms of iso-anomaly) far to the south on the Atlantic side of Cape Peninsula. Further, it may be equally abundant in warm waters of the Agulhas current on the east coast, as far north as Durban and probably beyond. This implies temperature tolerance throughout the range 10° to 23° C. at the least. The discontinuity in distribution off the south-west coast could, however, be due to a markedly stenohaline reaction on the part of *D. tripos*. The area from which we found it almost absent coincides with the low salinities observed northwards from the Orange river mouth throughout the area of maximum upwelling activity to Luderitz Bay and beyond.[1]

The point has been mentioned here because Schiller (1933) who has done so much to clear up the taxonomy of the Caudata group, added the trenchant note 'Ob immer stenohaline?' concerning the distribution of *D. tripos*, which suggests that this trait had already been noticed in other regions.

DIVERSITY OF THE MICROPLANKTON

The rich variety of the microplankton in the region surveyed may be judged from the list of all 208 categories recorded in the routine counts (Table 12). This table also shows their frequency of occurrence, and the frequency with which they occurred as dominants in each of the two separate ·series of thirty-nine stations, repeated at approximately the same positions, and in the smaller subsidiary series as shown by the column headings.

Table 12. *List of all microplankton categories recorded among routine counts, with data on their frequency of occurrence, and dominance, as shown by column headings*

Species or category	First survey 39 stations Present	Domi-nant	Second survey 39 stations (repeated) Present	Domi-nant	Six extra stations to south of main area Present	Domi-nant	Three extra stations to north of main area Present	Domi-nant	Four dis-coloured water-samples Present	>5%	Station W S 1076 (extra, no counterpart on first survey) Present	Domi-nant
DIATOMACEA												
Melosira sphaerica Karsten	2	—	—	—	—	—	—	—	—	—	—	—
Skeletonema costatum (Grev.) Cleve	1	o	3	1	—	—	—	—	—	—	—	—
Stephanopyxis palmeriana (Grev.) Grünow	—	—	—	—	1	—	—	—	—	—	—	—
S. turris (Grev. & Arnott) Ralfs	10	3	11	1	3	1	1	o	3	o	—	—
Thalassiosira condensata Cleve	5	o	—	—	4	2	1	1	—	—	—	—
T. excentrica Karsten	14	3	3	1	—	—	—	—	—	—	—	—
T. hyalinum (Grün.) Gran	4	o	—	—	—	—	—	—	—	—	—	—
T. rotula Meunier	1	o	—	—	—	—	—	—	—	—	—	—
T. subtilis (Ostenfeld) Gran	12	2	14	3	4	4	—	—	—	—	—	—
Thalassiosira spp. non det.	2	o	14	5	2	o	3	1	3	o	1	o
Bacterosira fragilis Gran	1	o	—	—	—	—	—	—	—	—	—	—
Coscinodiscus gigas Ehrenberg	1	o	—	—	1	o	—	—	—	—	—	—
C. janischii A. Schmidt	1	o	—	—	2	o	—	—	—	—	—	—
C. parvulus Karsten	1	o	—	—	—	—	—	—	—	—	—	—
C. radiatus Ehrenberg	1	o	—	—	—	—	—	—	—	—	—	—
Coscinodiscus spp. non det.	8	o	28	1	3	o	2	o	1	o	1	o
Actinocyclus spp. non det.	2	o	—	—	—	—	—	—	—	—	—	—
Planktoniella sol Wallich	19	6	24	9	6	1	2	o	—	—	—	—
Hemidiscus cuneiformis Wallich	1	o	2	o	—	—	2	o	—	—	—	—
Actinoptychus senarius Ehrenberg	2	o	6	o	—	—	2	o	—	—	1	o
Asterolampra spp. non det.	—	—	1	o	—	—	—	—	—	—	—	—
Asteromphalus heptactis (Brebisson) Ralfs	5	o	6	1	—	—	—	—	—	—	—	—
Biddulphia longicruris Greville	—	—	6	o	1	o	—	—	—	—	—	—
B. mobiliensis Bailey	—	—	—	—	2	o	—	—	—	—	—	—
B. regia (Schultze) Ostenfeld	—	—	—	—	1	o	1	o	—	—	—	—
Cerataulina pelagica (Cleve) Hendey	3	o	1	o	—	—	1	o	—	—	—	—
Triceratium favus Ehrenberg	1	o	—	—	1	o	—	—	—	—	—	—
Triceratium spp. non det.	—	—	—	—	1	o	—	—	—	—	—	—

[1] Here Dietrich (1950) has shown iso-lines of negative anomaly of 0·5–1·5 ‰ salinity, with normal values north and south, and but a little distance seaward.

Table 12 (*cont.*)

Species or category	First survey 39 stations		Second survey 39 stations (repeated)		Six extra stations to south of main area		Three extra stations to north of main area		Four dis-coloured water-samples		Station *WS 1076* (extra, no counterpart on first survey)	
	Present	Domi-nant	Present	Domi-nant	Present	Domi-nant	Present	Domi-nant	Present	>5%	Present	Domi-nant
DIATOMACEA												
Ditylum brightwelli (West) Grünow	·—	—	—	—	6	I	—	—	—	—	—	—
Hemialus hauckii Grünow	I	o	—	—	—	—	—	—	—	—	—	—
Eucampia cornuta (Cleve) Grünow	—	—	2	o	—	—	—	—	—	—	—	—
E. zoodiacus Ehrenberg	11	4	—	—	3	o	—	—	3	o	—	—
Chaetoceros affine Lauder	2	I	4	I	2	I	—	—	—	—	—	—
C. atlanticum Cleve	—	—	15	5	—	—	I	o	I	o	—	—
C. compressum Lauder	17	13	22	14	4	3	2	2	I	o	I	o
C. constrictum Gran	22	12	26	19	2	2	3	I	2	o	I	1
C. convolutum Castracane	17	7	22	5	5	o	2	I	—	—	—	—
C. costatum Pavilliard	4	4	I	o	—	—	—	—	—	—	I	o
C. curvatum Castracane	2	o	—	—	—	—	—	—	—	—	—	—
C. curvisetum Cleve	15	11	18	12	4	3	2	2	I	o	I	1
C. debile Cleve	4	3	4	2	1	1	—	—	—	—	1	1
C. decipiens Cleve	5	I	14	8	4	o	—	—	—	—	1	o
C. densum Cleve	·—	—	—	—	—	—	—	—	—	—	1	o
C. difficile Cleve	8	5	4	2	—	—	—	—	—	—	—	—
C. didymum Ehrenberg (vegetative phases)	12	6	10	2	1	o	2	1	I	o	—	—
C. didymum Ehrenberg (resting spores)	13	6	3	o	—	—	—	—	—	—	I	o
C. holsaticum Schütt	·—	—	3	o	—	—	—	—	—	—	—	—
C. imbricatum Mangin	I	o	—	—	—	—	—	—	—	—	—	—
C. laciniosum Sthütt	I	o	I	o	—	—	—	—	—	—	—	—
C. lorenzianum Grünow	2	o	14	9	—	—	2	I	—	—	—	—
C. parallelis Boden	—	—	I	o	—	—	—	—	—	—	—	—
C. peruvianum Brightwell	8	o	10	I	1	o	—	—	—	—	—	—
C. pseudocrinitum Ostenfeld	2	I	—	—	—	—	—	—	—	—	—	—
C. sociale Lauder	I	o	5	3	—	—	—	—	—	—	I	1
C. strictum Karsten	11	7	10	6	1	o	1	o	—	—	—	—
C. subsecundum (Grün.) Hustedt	11	3	3	o	—	—	—	—	—	—	—	—
C. subsecundum (Grün.) Hustedt (resting spores)	3	o	—	—	—	—	—	—	—	—	—	—
C. teres Cleve	15	7	2	o	—	—	—	—	—	—	—	—
C. tetras Karsten	4	I	2	2	—	—	—	—	—	—	—	—
C. van heurckii Gran	9	5	I	o	1	o	—	—	—	—	—	—
Chaetoceros spp. non det.	3	2	—	—	—	—	—	—	—	—	—	—
Bacteriastrum delicatulum Cleve	—	—	—	—	1	o	—	—	—	—	—	—
B. hyalinum Lauder	2	o	—	—	—	—	—	—	—	—	—	—
B. varians Lauder	I	o	2	o	2	I	—	—	—	—	—	—
Rhizosolenia alata Brightwell	23	6	22	5	5	o	2	o	—	—	—	—
R. cylindrus Cleve	—	—	I	o	—	—	1	o	—	—	—	—
R. fragilissima Bergon	I	o	—	—	—	—	—	—	—	—	—	—
R. hebetata (Bailey) Gran	26	12	18	7	—	—	3	o	—	—	—	—
R. imbricata Brightwell	7	I	13	2	1	o	3	o	—	—	—	—
R. robusta Norman ex Pritchard	3	o	—	—	—	—	—	—	—	—	—	—
R. setigera Brightwell	—	—	10	3	1	o	2	o	I	o	—	—
R. simplex Karsten	8	2	8	o	—	—	1	o	—	—	—	—
R. stolterfothii H. Peragallo	2	o	I	o	3	o	—	—	—	—	—	—
R. tyliformis Brightwell	7	o	17	11	2	o	3	2	—	—	—	—
Guinardia blavyana H. Peragallo	—	—	—	—	3	o	—	—	—	—	—	—
Guinardia sp. non det.	I	o	—	—	—	—	—	—	—	—	—	—
Leptocylindris danicus Cleve	5	2	2	o	—	—	—	—	—	—	—	—
Dactyliosolen mediterraneus H. Peragallo	7	I	10	6	—	—	2	2	—	—	—	—
Corethron criophilum Castracane	5	o	17	o	1	o	3	o	—	—	—	—
Fragilaria granulata Karsten	I	I	14	5	1	o	—	—	—	—	—	—
F. karsteni (Karsten) Boden	5	3	9	7	—	—	1	o	—	—	1	1
Asterionella japonica Cleve & Möller ex Gran	17	9	14	7	2	o	2	1	3	3	I	1
Thalassiothrix frauenfeldii (Grün.) Cleve & Grün.	—	—	—	—	—	—	1	o	—	—	—	—
T. longissima Cleve ex Grünow	22	6	29	10	2	o	2	o	—	—	—	—
Thalassionema nitzschioides (Grün.) Hustedt	I	o	7	I	5	2	1	o	—	—	—	—
Striatella sp. non det.	—	—	I	o	—	—	—	—	—	—	—	—
Achnanthes longipes Agardh	—	—	I	o	—	—	—	—	—	—	—	—
Navicula membranacea Cleve	—	—	I	o	—	—	—	—	—	—	—	—
Navicula spp. non det.	3	o	5	o	—	—	1	o	3	o	—	—
Pleurosigma capense Karsten	3	I	I	o	—	—	—	—	—	—	—	—
Pleurosigma sp. non det.	3	o	—	—	—	—	—	—	—	—	—	—
Nitzschia closterium (Ehrb.) Wm. Smith	10	2	6	o	1	o	—	—	—	—	I	o
N. delicatissima Cleve	19	14	21	9	2	I	3	o	3	o	—	—
N. longissima (Breb.) Ralfs	2	o	6	1	—	—	—	—	—	—	—	—
N. seriata Cleve	22	9	28	18	5	4	3	3	—	—	I	o

Table 12 (*cont.*)

Species or category	First survey 39 stations		Second survey 39 stations (repeated)		Six extra stations to south of main area		Three extra stations to north of main area		Four discoloured water-samples		Station WS 1076 (extra, no counterpart on first survey)	
	Present	Domi-nant	Present	Domi-nant	Present	Domi-nant	Present	Domi-nant	Present	>5%	Present	Domi-nant
DINOPHYCEAE												
Prorocentrum micans Ehrenberg	—	—	—	—	—	—	—	—	3	1	—	—
Prorocentrum sp. non det.	—	—	1	o	—	—	—	—	—	—	—	—
Palaeophalacroma verrucosum Schiller	1	o	—	—	—	—	—	—	—	—	—	—
Phalacroma Rudgei Murray & Whitting	1	o	—	—	—	—	—	—	—	—	—	—
P. argus Stein	—	—	1	o	—	—	—	—	—	—	—	—
P. minutum Cleve	1	o	—	—	1	o	—	—	—	—	—	—
Phalacroma spp. non det.	—	—	1	o	—	—	—	—	—	—	—	—
Dinophysis ovum Schütt	2	o	—	—	—	—	—	—	—	—	—	—
D. sphaerica Stein	—	—	—	—	1	o	—	—	—	—	—	—
D. acuminata Claparède & Lachmann	—	—	1	o	—	—	—	—	—	—	—	—
D. schröderi Pavillard	6	o	—	—	—	—	—	—	—	—	—	—
D. schüetii Murray & Whitting	1	o	—	—	—	—	—	—	—	—	—	—
D. tripos Gourret	4	o	6	o	6	4	—	—	—	—	—	—
Gymnodinium spp. non det.	3	o	1	o	—	—	—	—	1	o	—	—
Noctiluca miliaris Suriray	1	o	2	o	5	1	—	—	—	—	—	—
Warnowia sp. non det.	—	—	1	o	—	—	—	—	—	—	—	—
Blastodinium mangini Chatton	1	o	—	—	—	—	—	—	—	—	—	—
Blastodiniacea non det.	—	—	—	—	2	o	—	—	1	o	—	—
Ellopsidaceae non det.	—	—	1	o	—	—	—	—	—	—	—	—
Sphaerodinium sp. non det.	—	—	1	o	—	—	—	—	—	—	—	—
Peridinium triquetrum (Ehrb.) Lebour	—	—	—	—	—	—	—	—	3	3	—	—
P. crassipes Kofoid	3	1	—	—	—	—	—	—	—	—	—	—
P. depressum Bailey	1	o	—	—	—	—	—	—	—	—	—	—
P. elegans Cleve	2	o	—	—	—	—	—	—	—	—	—	—
P. oceanicum Vanhöffen	8	o	—	—	—	—	—	—	—	—	—	—
Peridinium spp. non det.	36	8	39	16	6	1	2	1	3	o	1	o
Goniaulax spinifera Clap. & Lachmann	14	6	2	o	—	—	—	—	—	—	—	—
Goniaulax sp. non det.	—	—	1	o	—	—	—	—	—	—	—	—
Pyrodinium sp. non det.	1	o	—	—	—	—	—	—	—	—	—	—
Amphidoma nucula Stein	1	o	—	—	—	—	—	—	—	—	—	—
Ceratium candelabrum (Ehrb.) Stein	13	1	4	o	3	o	—	—	—	—	—	—
C. furca (Ehrb.) Clap. & Lach.	11	o	10	o	6	o	—	—	—	—	—	—
C. pentagonum Gourret	—	—	4	o	—	—	—	—	—	—	—	—
C. lineatum (Ehrb.) Cleve	11	1	4	o	2	o	—	—	—	—	—	—
C. fusus (Ehrb.) Dujardin	24	2	19	o	5	o	2	o	—	—	—	—
C. tripos (O. F. Müller) Nitzsch	9	1	6	o	6	3	—	—	—	—	—	—
C. arietinum Cleve	19	1	12	o	1	o	2	o	—	—	—	—
C. limulus Gourret	—	—	7	o	—	—	—	—	—	—	—	—
C. platycorne von Daday	4	o	—	—	—	—	—	—	—	—	—	—
C. ranipes Cleve	—	—	—	—	1	o	—	—	—	—	—	—
C. vultur Cleve	—	—	—	—	4	o	—	—	—	—	—	—
C. buceros Zacharias	—	—	1	o	—	—	—	—	—	—	—	—
C. massiliense (Gourret) Jörgensen	—	—	6	o	5	o	1	o	—	—	—	—
C. macroceros (Ehrb.) Cleve	10	o	2	o	—	—	—	—	—	—	—	—
C. trichoceros (Ehrb.) Kofoid	1	o	3	o	—	—	—	—	—	—	—	—
Goniodoma polyedricum (Pouchet) Jörg.	2	o	—	—	—	—	1	o	—	—	—	—
Goniodoma sp. non det.	1	o	—	—	1	o	—	—	—	—	—	—
Small Dinophyceae non det.	—	—	—	—	—	—	—	—	2	o	—	—
OTHER PROTOPHYTA												
Trichodesmium thiebautii Gomont [filaments]	4	1	8	3	—	—	—	—	—	—	—	—
Phaeocystis sp. non det. [colonies]	—	—	—	—	1	o	—	—	—	—	—	—
Trochischia brachiolata (Möb.) Lemm.	—	—	1	o	—	—	—	—	—	—	—	—
T. multispinosa (Möb.) Lemm.	2	o	5	o	—	—	—	—	—	—	—	—
Halosphaera viridis Schmitz	2	o	—	—	—	—	—	—	—	—	—	—
Umbilicosphaera sp. non det.	—	—	1	o	—	—	—	—	—	—	—	—
Coccosphaeriales (other) non det.	4	o	11	o	2	o	—	—	—	—	—	—
Dictyocha fibula Ehrenberg	4	o	—	—	1	o	—	—	—	—	—	—
Distephanus speculum (Ehrb.) Haeckel	1	o	2	o	—	—	—	—	—	—	—	—
PROTOZOA												
Challengeridae	7	o	16	o	4	o	—	—	—	—	1	o
Acanthometridae	4	4	5	o	—	—	—	—	—	—	—	—
Radiolaria (other)	22	1	21	o	4	o	—	—	—	—	—	—
Foraminifera	24	3	33	7	4	o	2	o	—	—	—	—
Sticholonche sp. non det.	3	o	9	o	4	o	2	o	—	—	—	—
? *Cyclotrichium meunieri* Powers	—	—	—	—	—	—	—	—	1	1	—	—

Table 12 (cont.)

Species or category	First survey 39 stations		Second survey 39 stations (repeated)		Six extra stations to south of main area		Three extra stations to north of main area		Four dis-coloured water-samples		Station IIS 1076 (extra, no counterpart on first survey)	
	Present	Domi-nant	Present	Domi-nant	Present	Domi-nant	Present	Domi-nant	Present	>5	Present	Domi-nant
PROTOZA												
Ciliata (other, Tintinnids excepted)	—	—	4	0	—	—	—	—	—	—	—	—
Tintinnopsis spp.	4	0	2	0	1	0	—	—	—	—	—	—
Codonella spp.	1	0	17	1	—	—	2	0	—	—	—	—
Codonellopsis spp.	1	0	2	0	—	—	—	—	—	—	—	—
Favella spp.	—	—	1	0	—	—	—	—	—	—	—	—
Parafavella spp.	—	—	1	0	—	—	1	0	—	—	—	—
Epiplocylis spp.	10	0	11	0	—	—	—	—	—	—	—	—
Rhabdonella brandti Kofoid & Campbell	9	2	1	0	—	—	—	—	—	—	—	—
Rhabdonella spp.	10	1	4	0	—	—	—	—	—	—	—	—
Rhabdonellopsis spp.	2	0	1	0	—	—	—	—	—	—	—	—
Parundella spp.	—	—	3	0	—	—	—	—	—	—	—	—
Xystonella spp.	—	—	2	0	—	—	—	—	—	—	—	—
Xystonellopsis spp.	2	0	7	0	—	—	1	0	—	—	1	0
Undella spp.	6	0	7	0	—	—	—	—	—	—	—	—
Undellopsis tricollaria (Laackmann) K. & C.	1	0	—	—	—	—	—	—	—	—	—	—
Proplectella spp.	—	—	5	0	—	—	—	—	—	—	—	—
Dictyocysta spp.	20	2	13	0	—	—	2	0	—	—	—	—
Bursaopsis spp.	2	0	—	—	—	—	—	—	—	—	—	—
Amphorella spp.	2	0	2	0	—	—	—	—	—	—	—	—
Steenstrupiella spp.	—	—	—	—	—	—	2	0	—	—	—	—
Amphorellopsis spp.	—	—	1	0	—	—	—	—	—	—	—	—
Dadayiella spp.	—	—	6	0	—	—	1	0	—	—	—	—
Tintinnus lusus-undae Entz, Snr.	4	0	7	0	3	0	—	—	—	—	—	—
Salpingella spp.	2	0	1	0	—	—	—	—	—	—	—	—
Tintinnoinea (non det.)	10	0	1	0	3	0	—	—	2	0	—	—
METAZOA												
Diphyids (Siphonophora)	—	—	—	—	1	0	—	—	—	—	—	—
Chaetognatha	3	0	—	—	2	0	—	—	—	—	—	—
Polychaeta mainly larvae and post-larval	1	0	1	0	2	0	—	—	—	—	—	—
Ova: ? molluscan	2	1	—	—	—	—	—	—	—	—	—	—
Pteropoda: Limacina juv.	4	3	6	0	—	—	—	—	—	—	—	—
Pteropoda: ? Gymnosomata juv.	3	0	2	0	—	—	—	—	—	—	—	—
Post-larval lamellibranchs	—	—	1	0	3	0	—	—	—	—	—	—
Molluscan larvae, other	1	0	—	—	—	—	—	—	—	—	—	—
Ova: mainly Copepodan	21	10	28	3	3	0	1	0	1	0	—	—
Egg packets: mainly Harpacticid	22	3	16	1	3	0	2	0	—	—	—	—
Ova: Euphausian	2	1	?	0	—	—	—	—	—	—	—	—
Nauplii	37	16	37	14	6	2	2	1	—	—	—	—
Evadne nordmanni Lovén	—	—	—	—	1	0	—	—	—	—	—	—
Ostracoda	1	0	—	—	—	—	—	—	—	—	—	—
Copepoda	38	15	35	14	6	2	2	1	—	—	—	—
Cumacea	4	0	1	0	—	—	—	—	—	—	—	—
Euphausiidae: early larvae	1	0	5	0	3	0	—	—	—	—	—	—
Euphausiidae: late larvae → adult	—	—	3	0	—	—	—	—	—	—	—	—
Ophioplutei	1	0	—	—	—	—	—	—	—	—	—	—
Appendicularia	17	1	5	0	2	0	—	—	—	—	—	—
Doliolidae	2	0	—	—	2	0	—	—	—	—	—	—
Fish eggs	6	0	8	0	2	0	—	—	—	—	—	—
Fish larvae and post-larvae	6	0	8	0	2	0	—	—	—	—	—	—
SESTON												
Cast skins, etc.	9	4	32	10	6	1	3	0	1	0	—	—
Faecal pellets	15	7	27	4	4	0	1	0	—	—	1	0

From the full list, shorter series limited to the categories occurring as dominants (*a*) during both surveys, (*b*) during the first survey only, and (*c*) during the second survey only, have been abstracted in Table 13. Here the frequency data have been summarized in the form of double fractions. Thus the entry 'Stephanopyxis turris 10/3 and 11/1' signifies that this species was present at ten out of the thirty-nine stations of the first survey and dominant at three of those ten; present at eleven of the second survey stations, but dominant at only one of them.

This table provides most of the basis for selection of the relatively more important forms, without which detailed consideration of the vast mass of data on distribution and relative abundance could not usefully be attempted. It seemed best to insert it here, following immediately upon the full list from which it has been derived, although the further consideration of individual species—distributions, etc. in which it has been utilized is deferred until after the description of main group distribution.

Tables 12 and 13 suffice to bring out one important difference between the rich diatom-flora of this typical subtropical upwelling region, and that of other sea areas where diatoms predominate, such as the antarctic zone of the southern ocean. The colder water flora and that of the Benguela current have alike been described as 'monotonous' (in a restricted sense) since the one class of algae predominates in both of them. The colder water flora, however, tends to be characterized by a more extreme monotony, in that one or two species are frequently found to predominate over all the others to a very marked degree, over wide areas and for long periods of time (Hart, 1934; Marumo, 1953). The Benguela current samples are very much more varied, as shown by the large number of species recorded as dominants on the criterion chosen here. Even if we apply the criterion used by the Japanese—least number of species needed to attain 50% of the total cell count—the diversity of the Benguela samples would be more than twice as great as that of many antarctic ones, at least five or six species being needed to attain this proportion in most of the catches. Indeed, when we consider the occasional predominance of dinoflagellates, and of *Trichodesmium* at some of the poorer stations, and the fact that such nannoplankton forms as Coccosphaeriales and small dinoflagellates would certainly bulk far more largely had it been practicable to use other sampling methods, it seems very doubtful whether this plankton should be regarded as 'monotonous', even in the restricted sense.

Table 13. *Abridged frequency data: Categories occurring as dominants at one or more of the thirty-nine repeated stations*

(a) During both surveys		(b) During the first survey only		(c) During the second survey only	
Stephanopyxis turris	10/3 and 11/1	Eucampia zoodiacus	11/4 and 0/0	Skeletonema costatum	1/0 and 3/1
Thalassiosira excentrica	14/3 and 3/1	Chaetoceros costatum	4/4 and 1/0	Thalassiosira spp. non det.	2/0 and 14/5
T. subtilis	12/2 and 14/3	C. didymum (resting spores)	13/6 and 3/0	Coscinodiscus spp. non det.	8/0 and 28/1
Planktoniella sol	19/6 and 24/9	C. pseudocrinitum	2/1 and 0/0	Asteromphalus heptactis	5/0 and 6/1
Chaetoceros affine	2/1 and 4/1	C. subsecundum	11/3 and 3/0	Chaetoceros atlanticum	0/0 and 15/5
C. compressum	17/13 and 24/9	C. teres	15/7 and 2/0	C. lorenzianum	2/0 and 14/9
C. constrictum	22/12 and 26/19	C. van heurckii	9/5 and 1/0	C. peruvianum	8/0 and 10/1
C. convolutum	17/7 and 22/5	Chaetoceros spp. non det.	3/2 and 0/0	C. sociale	1/0 and 5/3
C. curvisetum	15/11 and 18/12	Rhizosolenia simplex	8/2 and 8/0	Rhizosolenia setigera	0/0 and 10/3
C. debile	4/3 and 4/2	Leptocylindrus danicus	5/2 and 2/0	R. styliformis	7/0 and 17/11
C. decipiens	5/1 and 14/8	Pleurosigma capense	3/1 and 1/0	Thalassionema nitzschioides	1/0 and 7/1
C. difficile	8/5 and 14/2	Nitzschia closterium	10/2 and 6/0	Nitzschia longissima	2/0 and 6/1
C. didymum (vegetative phases)	12/6 and 10/2	Peridinium crassipes	3/1 and 0/0	Codonella spp.	1/0 and 17/1
C. strictum	11/7 and 10/6	Goniaulax spinifera	14/6 and 2/0		
C. tetras	4/1 and 2/2	Ceratium candelabrum	13/1 and 4/0		
Rhizosolenia alata	23/6 and 22/5	C. lineatum	11/1 and 4/0		
R. hebetata	26/12 and 18/7	C. fusus	24/2 and 19/0		
R. imbricata	7/1 and 13/2	C. tripos	9/1 and 6/0		
Dactyliosolen mediterraneus	7/1 and 10/6	C. arietinum	19/1 and 12/0		
Fragilaria granulata	1/1 and 14/5	Acanthometridae	4/4 and 5/0		
F. karsteni	5/3 and 9/7	Radiolaria (other)	22/1 and 21/0		
Asterionella japonica	17/9 and 14/7	Rhabdonella brandtii	9/2 and 1/0		
Nitzschia delicatissima	19/14 and 21/9	Rhabdonella spp.	10/1 and 4/0		
N. seriata	22/9 and 28/18	Dictyocysta spp.	20/2 and 13/0		
Peridinium spp. non det.	36/8 and 39/16	Ova, ? molluscan	2/1 and 0/0		
Trichodesmium thiebautii	4/1 and 8/3	Pteropoda: Limacina juv.	4/3 and 6/0		
Foraminifera	24/3 and 33/7	Ova: Euphausian	2/1 and 0/0		
Ova, mainly Copepodan	21/10 and 28/3	Appendicularia	17/1 and 5/0		
Egg packets, mainly Harpacticid	22/3 and 16/1				
Nauplii	37/16 and 37/14				
Copepoda	38/15 and 35/14				
Cast skins, etc.	9/4 and 32/10				
Faecal pellets	15/7 and 27/4				

Table 14. First survey (autumn). Estimated numbers of the main groups and total microplankton.

Station no.	Approx. distance from land in sea-miles	Settlement volumes (ml.)	Fractions examined	No. of categories	I Bacillariophyceae Estimated totals	I % of IV	I % of VIII	II Dinophyceae Estimated totals	II % of IV	II % of VIII	III Other plants Estimated totals	III % of IV	III % of VIII	IV Phytoplankton: Σ(I+II+III) Estimated totals	IV % of VIII	V Protozoa Estimated totals	V % of VIII	VI Metazoa Estimated totals	VI % of VIII	VII Seston Estimated totals	VII % of VIII	VIII Estimated microplankton totals
WS 964	103	7	1/724	27	73,124	68.2	36.7	34,028	31.8	17.1	—	—	—	107,152	53.8	52,852	26.6	39,096	19.6	—	—	199,100
WS 965	90	5	1/600	26	143,400	85.4	59.8	24,800	14.6	10.2	—	—	—	168,000	70.0	40,800	17.0	31,200	13.0	—	—	240,000
WS 966	77	8	1/1250	35	363,750	86.4	72.2	56,250	13.3	11.1	1,250	0.3	0.3	421,250	83.6	70,000	13.9	12,500	2.5	—	—	503,750
WS 967	61	11	1/10,000*	44	1,634,250	98.3	95.9	25,750	1.6	1.5	250	0.1	0.1	1,660,250	97.5	14,250	0.8	29,500	1.7	—	—	1,704,000
WS 968	43	10	1/750	29	22,500	28.8	16.3	55,500	71.2	40.2	—	—	—	78,000	56.5	18,750	13.6	41,250	29.9	—	—	138,000
WS 969	28	15	1/3,168	38	4,118,400	96.2	94.2	161,568	3.8	3.7	—	—	—	4,279,968	97.8	25,344	0.6	66,528	1.5	—	—	4,371,840
WS 970	12	8	1/250, 1/2,000	47	1,382,500	89.0	79.3	170,000	11.0	9.7	—	—	—	1,552,500	89.0	38,000	2.2	154,000	8.8	—	—	1,744,500
WS 971	30	9	1/2,000	29	386,000	58.2	46.5	262,000	41.8	33.1	—	—	—	648,000	79.6	60,000	7.7	100,000	12.7	—	—	808,000
WS 972	53	5	1/3,000	24	972,000	64.3	60.4	546,000	35.7	34.0	—	—	—	1,518,000	94.4	12,000	0.7	78,000	4.9	—	—	1,608,000
WS 973	72	8	1/2,000	25	1,010,000	61.8	58.8	624,000	38.2	36.1	—	—	—	1,634,000	95.1	12,000	0.7	72,000	4.2	—	—	1,718,000
WS 974	93	10	1/100	24	314,000	84.0	65.1	60,000	16.0	12.5	—	—	—	374,000	77.6	22,000	4.6	86,000	17.8	—	—	482,000
WS 975	112	6	1/2,000	24	202,000	63.5	51.8	116,000	36.5	29.3	—	—	—	318,000	81.1	62,000	15.8	12,000	3.1	—	—	392,000
WS 976	142	6	1/2,000	24	282,000	91.4	53.2	26,000	8.6	4.9	—	—	—	308,000	58.1	164,000	30.9	58,000	10.9	—	—	530,000
WS 977	106	13	1/2,000	25	212,000	83.5	46.7	40,000	15.7	8.8	2,000	0.8	0.4	254,000	55.9	112,000	24.7	88,000	19.4	—	—	454,000
WS 978	81	28	1/2,400	30	816,600	79.9	58.4	199,200	19.6	14.4	4,800	0.5	0.3	1,017,600	73.1	290,400	20.9	84,000	6.0	—	—	1,392,000
WS 979	48	45	1/8,000, 1/192,000	31	98,328,000	99.9	99.8	50,000	<0.01	<0.01	8,000	<0.01	<0.01	98,392,000	99.9	16,000	<0.01	32,000	<0.01	—	—	98,440,000
WS 980	20	30	1/8,000, 1/64,000	28	45,344,000	98.9	98.2	512,000	1.1	1.1	—	—	—	45,856,000	93.3	—	—	320,000	0.7	—		46,176,000
WS 981	11	15	1/900, 1/21,600	31	9,987,300	98.1	97.0	196,200	1.9	1.9	—	—	—	10,183,500	98.9	25,200	0.2	86,400	0.8	—	—	10,295,100
WS 982	10	130	1/180,000	27	74,070,000	99.2	98.7	612,000	0.8	0.8	—	—	—	74,682,000	99.5	96,000	0.1	246,000	0.3	—	—	75,024,000
WS 983	31	28	1/600, 1/72,000	25	40,180,800	99.6	97.9	144,000	0.4	0.3	—	—	—	40,324,800	98.2	600	<0.01	720,000	1.8	—	—	41,045,400
WS 984	46	64	1/96,000*	25	69,432,000	99.9	99.2	54,000	0.1	0.1	—	—	—	69,486,000	99.3	120,000	0.2	240,000	0.3	96,000	0.2	69,942,000
WS 985	71	40	1/3,000, 1/3,600	25	27,477,000	99.8	99.5	42,000	0.2	0.1	—	—	—	27,519,000	99.6	18,000	0.1	69,000	0.3	6,000	<0.01	27,612,000
WS 986	90	?10	1/300, 1/500	32	97,300	73.0	47.6	35,700	26.8	17.5	300	0.2	0.1	133,300	65.2	5,600	2.7	65,400	31.5	—	—	204,300
WS 987	59	14	1/300	18	11,400	16.2	6.6	58,800	83.8	33.9	—	—	—	70,200	40.5	6,900	4.0	62,100	35.8	34,200	19.7	173,400
WS 988	22	100	1/45,000, 1/300,000	19	270,450,000	100.0	99.9	—	—	—	—	—	—	270,450,000	99.9	—	—	360,000	0.1	—	—	270,810,000
WS 989	8	67	1/9,000, 1/216,000	31	158,508,000	99.9	99.8	135,000	0.1	<0.01	—	—	—	158,643,000	99.9	36,000	<0.01	63,000	<0.01	36,000	<0.01	158,778,000
WS 990	22	55	1/9,600	27	74,006,400	99.8	99.6	182,400	0.2	0.2	—	—	—	74,188,800	99.8	38,400	<0.01	57,600	0.1	38,400	0.1	74,323,200
WS 991	38	185	1/450,000, 1/1,200	13	258,300,000	100.0	99.8	—	—	—	—	—	—	258,300,000	99.8	—	—	450,000	0.2	—	—	258,750,000
WS 992	52	30	1/6,000	33	50,692,800	99.1	98.8	268,800	0.5	0.5	192,000	0.4	0.3	51,153,600	99.6	31,200	0.1	57,600	0.1	86,400	0.2	51,328,800
WS 993	66	9	1/300	40	19,800	68.0	28.3	6,600	22.7	9.4	2,700	9.3	3.9	29,100	41.6	3,300	4.7	33,300	47.7	4,200	6.0	69,900
WS 994	87	8	1/300	35	16,800	69.1	21.1	5,400	22.2	6.8	2,100	8.7	2.6	24,300	30.5	2,100	2.6	40,200	50.4	13,200	16.5	79,800
WS 995	100	6	1/300	29	12,300	58.6	13.4	8,100	38.6	8.9	600	2.8	0.7	21,000	23.0	7,500	8.2	56,100	61.3	6,900	7.5	91,500
WS 996	130	4	1/200	33	16,000	70.8	29.5	3,200	14.2	5.9	3,400	15.0	6.3	22,600	41.7	4,000	7.5	24,800	45.7	2,800	5.1	54,200
WS 997	97	6	1/300	29	13,800	82.1	27.7	900	5.4	1.8	2,100	12.5	4.3	16,800	33.8	3,000	6.0	23,700	47.5	6,300	12.7	49,800
WS 998	78	4	1/250	16	3,000	85.7	13.3	500	14.3	2.2	—	—	—	3,500	15.5	1,000	4.5	12,250	54.5	5,750	25.4	22,500
WS 999	59	4	1/200	16	1,200	50.0	3.3	1,200	50.0	3.3	—	—	—	2,400	6.6	3,000	8.2	16,800	45.9	14,400	39.3	36,600
WS 1000	37	6	1/300	13	42,300	95.9	49.0	1,800	4.1	2.0	—	—	—	44,100	51.0	7,200	8.3	20,100	23.4	15,000	17.3	86,400
WS 1001	20	50	1/18,000, 1/36,000	13	7,758,000	99.5	98.1	36,000	0.5	0.5	—	—	—	7,794,000	98.6	—	—	72,000	0.9	36,000	0.5	7,902,000
WS 1002	8	110	1/36,000, 1/62,000	10	43,710,000	99.6	99.6	108,000	0.4	0.3	—	—	—	43,818,000	99.9	—	—	72,000	0.1	—	—	43,890,000

* And larger fractions for the larger organisms.

DISTRIBUTION OF THE MAIN GROUPS OF MICROPLANKTON

First survey

The estimated numbers of the main groups of microplankton present in the hauls from each station are given in Table 14, with the approximate distances of the stations from the nearest point on the coast. The fractions examined, number of species or other categories recognized in each count, and the settlement volumes of the catches are also given, together with percentages of the main groups relative to the totals, as shown by the column headings. These data, excepting the percentages, are also shown graphically in Figs. 58–64, designed to aid general description of the results on each separate line of stations.
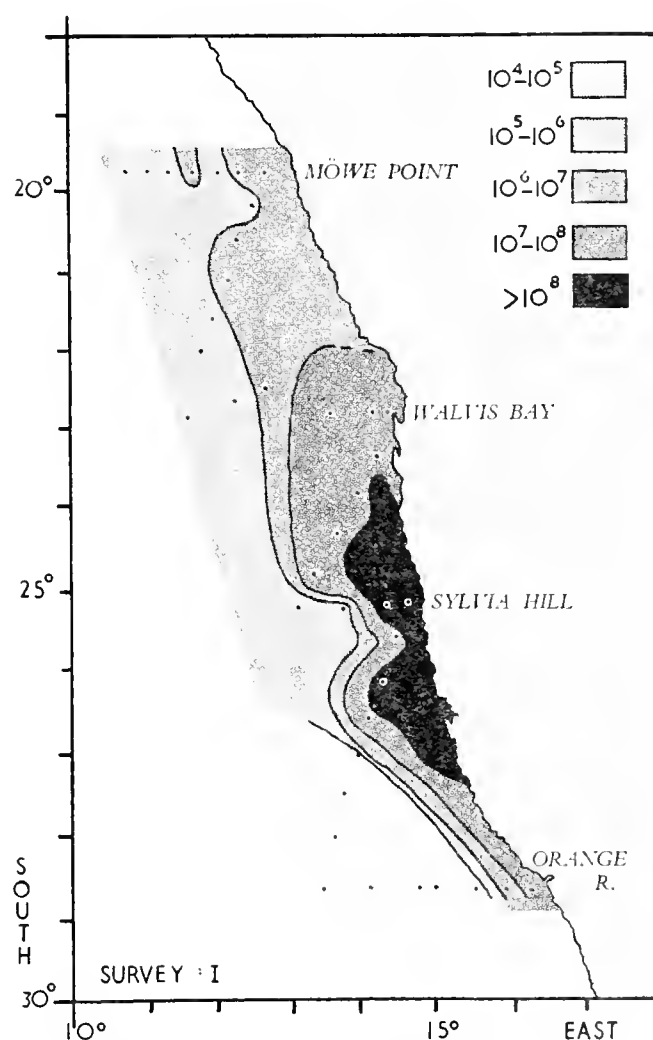
Fig. 57. Distribution of the microplankton, estimated totals per net haul, survey I, March 1950.
(Station numbers are shown in Fig. 1.)

Fig. 57 shows the estimated microplankton totals in the first survey contoured logarithmically. From this the concentration of the heaviest catches in the coastal waters, more particularly in the centre of the region, is quite clear. The zone of rich coastal microplankton was narrow in the south, off the mouth of the Orange river, and reached its greatest extent seawards off Walvis Bay. The increase in width of the zone with decreasing latitude up to this point was interrupted by one deep constriction at the seaward end of the Sylvia Hill line. North of Walvis Bay the coastal microplankton was much less abundant, though still richer, especially in phytoplankton, than that of the offshore waters. The

coastal zone also narrowed again to the north, and off Möwe Point the general tendency of diminishing quantity of microplankton with increasing distance from land was somewhat obscured by the presence of relatively poor isolated catches within the coastal region. The hydrological data and qualitative plankton observations combine to show that these were due to actual tongue-like intrusions or isolated patches of more oceanic surface-water (see pp. 157, 246), with inherently poorer plankton content, and not merely to local impoverishment of the coastal water population. It would seem that the Möwe Point line was near the northern limit of the main region of upwelling at the time of this survey, and that some inter-digitation of the distinctive types of surface-water (and even some overlapping of these in the vertical plane) was the result. Such effects, well known to occur on a large scale near the
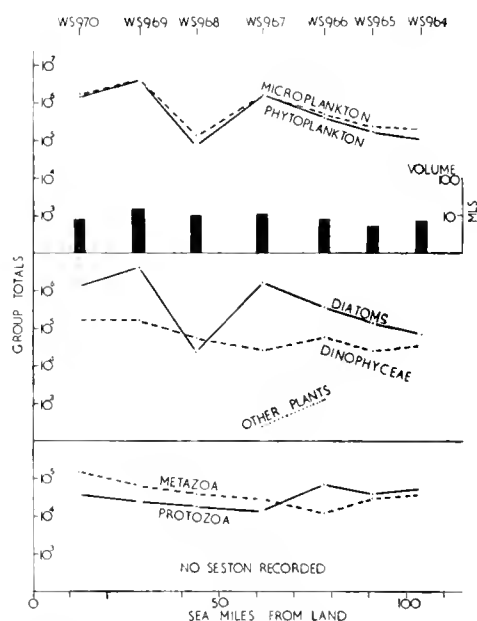
Fig. 58. Distribution of main groups of microplankton, estimated totals per net haul. Möwe Point line, survey I, 4–5 March 1950. The histogram shows the settled volumes of the catch in millimetres.
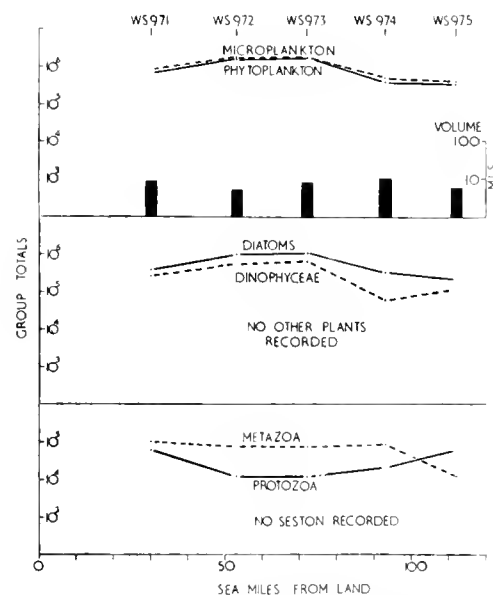
Fig. 59. Distribution of main groups of microplankton, estimated totals per net haul, survey I, Northern Intermediate line, 5 March 1950.

northern limits of the analogous Peru coastal current, must necessarily affect any simplified presentation of data collected with an arbitrarily chosen spatial limit, and plotted on the horizontal plane only, as here.

Inshore on the Sylvia Hill line the two innermost stations show, as did the stations inshore on the Walvis Bay and mid-intermediate lines, the heaviest concentrations of phytoplankton. According to the hydrological evidence (p. 162) these occur in old and rather mixed upwelled water. The two outermost stations on the Sylvia Hill line present a strong contrast. The phytoplankton, in quantity more characteristic of oceanic water, consisted of a rather neutral mixture of coastal and oceanic species. The hydrological evidence we have seen tends to link these two stations with more purely coastal water farther to the south, but the relatively high salinities and the salinity section (Fig. 15) in particular, suggest that they may lie in rather mixed oceanic water, into which some very recent upwelling was introducing a pattern of vertical layering.

One other distributional feature well shown in Fig. 57—the extreme poverty of the microplankton offshore in the south of the area, even at moderate distances from land—is much more difficult to understand. The point is reconsidered later when the results from the Orange river line are described in detail.

From Fig. 58 it can be seen that, on the Möwe Point line, the quantities of all main groups excepting Protozoa were highest inshore, with a pronounced falling off at the third station seawards, some slight secondary increase farther out and then a general decrease, most marked among the diatoms, to the low oceanic values at the seaward end of the line. 'Other plants' were observed in very small numbers some distance offshore, but not at the two outermost stations. The proportion of Dinophyceae to diatoms was above the average for the whole survey area, and Seston was not noted at the dilutions necessary to obtain counts. The relative abundance of Protozoa here was due mainly to large Radiolaria and especially tintinnids. The total estimated numbers of microplankton were relatively small throughout.

It should be noted that the stations have been plotted so that the distance scale from the land seawards reads from the left of the page, regardless of chronological sequence. This has been done so as to secure uniformity of treatment throughout the series of diagrams (Figs. 58–64, 66–72).
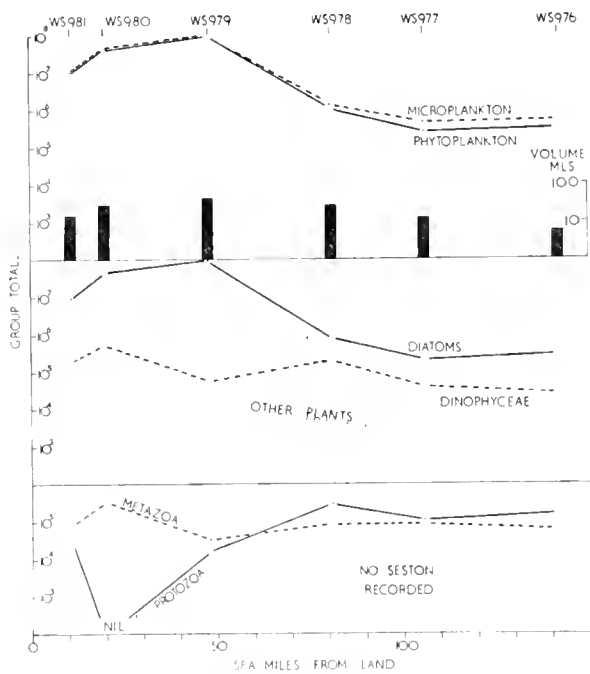
Fig. 60. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Walvis Bay line, 6–8 March 1950.
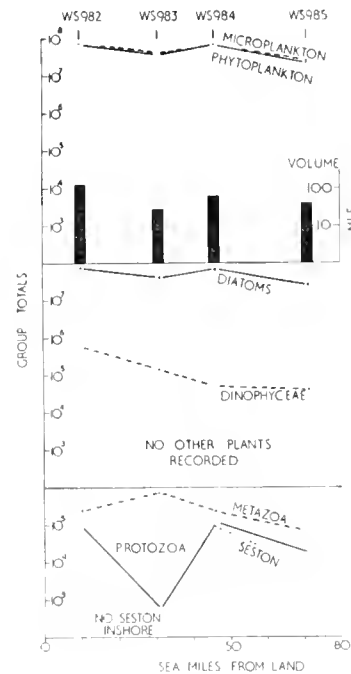
Fig. 61. Distribution of the main groups of micro-plankton, estimated totals per net haul, survey I, Middle–Intermediate line, 9–10 March 1950.

On the northern intermediate line the quantities of microplankton were still small and rather uniform, greatest at a moderate distance out towards the shelf-edge and least, owing mainly to the usual drop in diatom numbers, at the station farthest offshore. The proportion of Dinophyceae to diatoms was unusually high, and it will be shown later that local abundance of *Goniaulax spinifera* was mainly responsible for this. Neither 'other plants' nor Seston were observed on this line.

Conditions more typical of the Benguela current proper were first encountered on the Walvis Bay line (Fig. 60). Here the vastly greater quantities of diatoms in the inshore waters and their abrupt decrease seawards are even reflected in the settlement volumes. (The latter are rarely a reliable guide to plankton quantities, being frequently distorted by differential packing among organisms of diverse shapes, the presence of small numbers of extra large organisms, and the necessity of settling out large samples in relatively wide cylinders, so that the volumes cannot be read with the same accuracy as the small ones.) They are included only for their value as a basis for crude comparison with earlier collections in other areas, from some of which numerical estimates are not yet available.
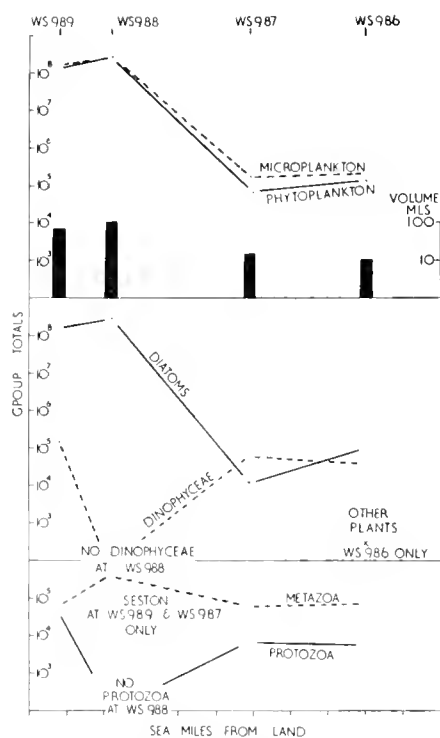
Fig. 62. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Sylvia Hill line, 10-11 March 1950.
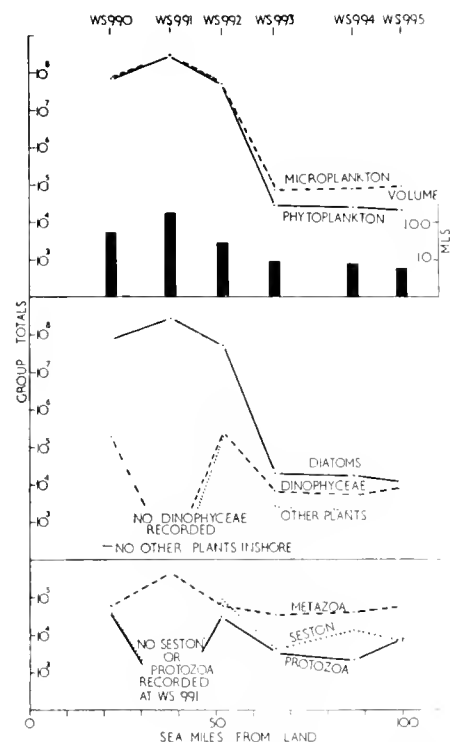
Fig. 63. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Southern Intermediate line, 11–12 March 1950.
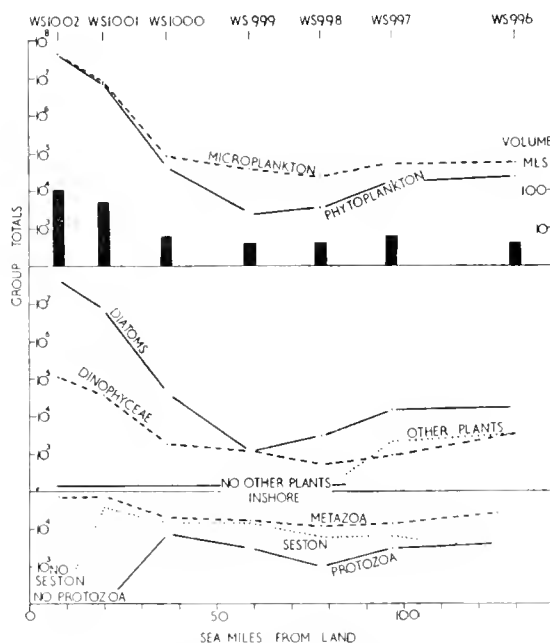
Fig. 64. Distribution of the main groups of microplankton, estimated totals per net haul, survey I, Orange river line, 12–14 March 1950.

On the Walvis Bay line Protozoa and Metazoa were present only in very moderate numbers, their *relative* importance greatly increasing beyond the point where the rich diatom plankton declined. Yet again this transition zone was the only point where 'other plants' were noted.

Rich inshore conditions persisted right out to the seaward end of the short mid-intermediate line, with large volumes, very large numbers of diatoms, and relatively few Dinophyceae (Fig. 61).

Seston was recorded at the two outer stations, the first time it had been observed (in the very small fractions used to obtain microplankton counts) during this first survey.

The Sylvia Hill line (Fig. 62) showed extreme contrast between the two diatom-rich inshore stations, and the impoverished offshore stations, where Dinophyceae were almost as numerous as the diatoms.

Again, the southern intermediate line (Fig. 63) showed very similar conditions; a heavy diatom-rich microplankton inshore; while offshore, though all the other groups showed some slight falling off in numbers from the third station seaward (where diatoms still predominated) the relative importance of those other groups was much greater in the smaller catches.

Finally, on the Orange river line (Fig. 64) the rich diatom plankton of the two inshore stations contrasted strongly with extremely small quantities of phytoplankton offshore, though moderate numbers of Protozoa, Metazoa and considerable quantities of Seston were recorded there. The capture of large numbers of herbivorous zooplankton especially the Pteropod *Limacina bulimoides* at these offshore stations, and the large quantity of Seston present, suggested that recent intensive grazing may have reduced a richer phytoplankton offshore not long before the stations were worked; because the greater width of the continental shelf at this point would lead one to expect greater seaward extension of the rich inshore conditions here at most times. The zooplankton data derive from the sorting of material from nets of coarser mesh, so that this point cannot be indicated in the uniform series of diagrams.

Second survey

Primary data concerning groups totals, relative percentages, etc., for the microplankton samples obtained during the second survey are given in Table 15. This has been constructed so that the sequence of stations, and of the lines of stations, follows that of the corresponding observations made during the first survey, regardless of their chronological order (cf. Table 14).

The total microplankton estimates for the second survey, contoured logarithmically in Fig. 65 (corresponding to Fig. 57 for the first survey) show an underlying similarity of distribution, consistent with the idea that upwelling activity proceeds (doubtless with minor fluctuations in intensity) throughout most of the year, over the major part of the area. Except in the extreme south, where the observations on the Orange river line are anomalous, rich catches inshore with rapid decrease in quantity as one proceeded seawards was the general rule. The heaviest catches of all were again obtained off Sylvia Hill and Luderitz Bay, and yet again an incursion of offshore water with contrastingly poor plankton was evident immediately seawards of the richest area, suggesting recurrence of the swirl centred (perhaps) to the south of the one encountered here during the first survey. A tongue-like intrusion of sparsely populated oceanic water in the north, on the Möwe Point line, was even more clearly defined than during the first survey, owing to the working of three extra stations to the north of the repeated series.

With all these points of resemblance to the distribution observed during the first survey there are still some differences, showing that even within a current-system apparently so persistent throughout most of the year, some seasonal changes affect the plankton population. Thus during the second survey the region of rich coastal plankton was smaller and did not extend so far seaward, especially off Walvis Bay. Conversely, the offshore microplankton, though still much more scanty than that to be found inshore, was generally somewhat richer than it had been during the first survey, especially to the north. Indeed, on the Möwe Point line (Fig. 66) only the station farthest inshore was appreciably richer in diatoms than those near the seaward end of the line. 'Other plants' were recorded only near the apparent transition point between the rapidly dwindling coastal plankton and the seasonally

Table 15. Second survey (spring). Estimated numbers of the main groups and total microplankton

Station no.	Approx. distance from land in sea-miles	Settlement volumes (ml.)	Fractions examined	No. of categories	I Bacillariophyceae Estimated totals	% of IV	% of VIII	II Dinophyceae Estimated totals	% of IV	% of VIII	III Other plants Estimated totals	% of IV	% of VIII	IV Phytoplankton Σ(I+II+III) Estimated totals	% of VIII	V Protozoa Estimated totals	% of VIII	VI Metazoa Estimated totals	% of VIII	VII Seston Estimated totals	% of VIII	VIII Estimated microplankton totals
WS 1102	110	10	1/3,000	40	1,734,000	94.9	84.1	93,000	5.1	4.5	—	—	—	1,827,000	88.6	111,000	5.5	102,000	4.9	21,000	1.0	2,061,000
WS 1101	91	15	1/6,000	38	5,208,000	98.6	96.6	72,000	1.4	1.3	—	—	—	5,280,000	97.9	54,000	1.0	54,000	1.0	6,000	0.1	5,394,000
WS 1100	75	18	1/9,000	31	4,968,000	94.1	92.3	153,000	5.9	2.9	—	—	—	5,121,000	95.2	108,000	2.0	126,000	2.3	27,000	0.5	5,382,000
WS 1099	64	7	1/900	38	185,400	80.8	55.2	42,300	18.4	12.6	1,800	0.8	0.5	229,500	68.3	29,700	8.9	63,000	18.8	13,500	4.0	335,700
WS 1098	47	12	1/6,000	27	2,082,000	95.9	85.0	90,000	4.1	3.7	—	—	—	2,172,000	88.7	96,000	3.9	108,000	4.4	72,000	3.0	2,448,000
WS 1097	31	8	1/3,000	32	1,398,000	94.3	83.7	84,000	5.7	5.0	—	—	—	1,482,000	88.7	36,000	2.2	129,000	7.7	24,000	1.4	1,671,000
WS 1096	14	25	1/24,000	22	19,320,000	99.7	99.0	48,000	0.3	0.3	—	—	—	19,368,000	99.3	120,000	0.6	24,000	0.1	—	—	19,512,000
WS 1093	33	10	1/3,600	34	3,618,000	95.3	89.1	180,000	4.7	4.4	—	—	—	3,798,000	93.5	75,600	1.9	122,400	3.0	64,800	1.6	4,060,800
WS 1091	58	6	1/2,700	36	969,300	95.5	88.0	45,000	4.5	4.4	—	—	—	1,015,200	92.2	24,300	2.2	51,300	4.6	10,800	1.0	1,101,600
WS 1090	82	12	1/3,000	35	1,317,000	97.1	85.1	36,000	2.7	2.3	3,000	0.2	0.2	1,356,000	87.6	48,000	3.1	126,000	8.1	18,000	1.2	1,548,000
WS 1089	101	6	1/900	28	117,000	72.6	35.2	44,100	27.4	13.3	—	—	—	161,100	48.5	37,800	11.4	109,800	33.1	23,400	7.0	332,100
WS 1088	117	12	1/1,500	29	1,159,500	91.2	85.0	111,000	8.7	8.1	1,500	0.1	0.1	1,272,000	93.2	25,500	1.9	52,500	3.9	13,500	1.0	1,363,500
WS 1080	144	6	1/2,700	36	483,300	91.9	78.5	42,300	8.1	6.9	—	—	—	525,600	85.4	38,700	6.3	36,900	6.0	14,400	2.3	615,600
WS 1081	117	10	1/900	26	405,000	82.0	66.0	86,400	17.5	14.1	2,700	0.5	0.4	494,100	80.5	86,400	14.1	14,400	2.3	18,900	3.1	613,800
WS 1079	83	38	1/4,500	31	1,962,000	95.4	82.5	90,000	4.4	3.8	4,500	0.2	0.2	2,056,500	86.5	117,000	4.6	121,500	5.1	81,000	3.8	2,376,000
WS 1078	48	22	1/1,500	15	25,500	51.5	10.7	24,000	48.5	10.1	—	—	—	49,500	20.8	24,000	10.1	105,000	44.0	60,000	25.1	238,500
WS 1077	21	9	1/600	35	402,600	96.1	86.1	10,200	2.4	2.2	6,000	1.5	1.3	418,800	89.6	10,800	2.3	26,400	5.6	11,400	2.5	467,400
WS 1075	10	16	1/900	29	22,923,000	99.3	98.6	153,000	0.6	0.6	18,000	0.1	0.1	23,094,000	99.3	54,000	0.2	72,000	0.4	27,000	0.1	23,247,000
WS 1074	14	10	1/3,000	28	11,835,000	99.6	98.5	36,000	0.3	0.3	18,000	0.1	0.1	11,889,000	98.9	33,000	0.2	48,000	0.4	60,000	0.5	12,030,000
WS 1073	30	10	1/1,500	31	87,000	64.4	28.7	46,500	34.4	15.4	1,500	1.2	0.5	135,000	44.6	25,500	8.4	105,000	34.6	37,500	12.4	303,000
WS 1072	48	11	1/2,400	38	820,800	92.7	75.7	62,400	7.0	5.7	2,400	0.3	0.2	885,600	81.6	48,000	4.4	108,000	10.0	43,200	4.0	1,084,800
WS 1071	73	15	1/3,000	37	2,694,000	98.4	91.8	42,000	1.5	1.5	3,000	0.1	0.1	2,739,000	93.4	36,000	1.2	123,000	4.2	36,000	1.2	2,934,000
WS 1070	94	15	1/2,400	36	1,941,600	97.6	88.5	48,000	2.4	2.2	—	—	—	1,989,600	90.9	33,600	1.5	120,000	5.5	45,600	2.1	2,188,800
WS 1069	58	16	1/600, 1/3,000	45	840,600	64.4	57.5	112,800	11.8	7.7	1,800	0.2	0.1	955,200	65.3	92,400	6.3	366,600	25.1	47,400	3.3	1,461,600
WS 1064	26	50	1/90,000	22	67,950,000	99.2	98.8	450,000	0.7	0.7	90,000	0.1	0.1	68,490,000	99.6	—	—	90,000	0.1	180,000	0.3	68,760,000
WS 1063	10	160	1/30,000, 1/300,000	27	312,300,000	99.8	99.8	450,000	0.2	0.1	—	—	—	312,750,000	99.9	30,000	<0.1	30,000	<0.1	120,000	<0.1	312,930,000
WS 1062	22	175	1/40,000, 1/1,400,000	23	258,680,000	99.9	99.7	80,000	<0.1	<0.1	80,000	<0.1	<0.1	258,840,000	99.8	160,000	0.1	80,000	<0.1	80,000	<0.1	259,160,000
WS 1061	28	20	1/24,000	24	27,264,000	99.3	98.9	168,000	0.7	0.7	—	—	—	27,432,000	99.6	72,000	0.2	72,000	0.2	—	—	27,576,000
WS 1060	46	18	1/12,000	24	10,740,000	99.5	97.5	48,000	0.4	0.4	12,000	0.1	0.1	10,800,000	98.0	96,000	0.9	96,000	0.9	24,000	0.2	11,016,000
WS 1059	65	15	1/600	34	199,800	49.9	44.8	12,000	3.0	2.7	189,000	47.1	42.4	400,800	89.9	7,800	1.7	30,600	6.9	6,600	1.5	445,800
WS 1058	80	15	1/1,200	37	416,400	54.6	49.2	10,800	1.4	1.3	334,800	44.0	39.6	762,000	90.1	25,200	3.0	49,200	5.8	9,600	1.1	846,000
WS 1057	97	35	1/620	34	161,200	64.7	48.8	16,120	6.5	4.9	71,920	28.8	21.8	249,240	75.5	11,760	3.6	45,880	13.8	23,560	7.1	330,460
WS 1056	128	45	1/13,200	29	6,375,600	94.9	93.2	66,000	1.0	1.0	277,200	5.1	4.0	6,718,800	98.2	30,600	0.6	52,800	0.8	26,400	0.4	6,837,600
WS 1055	94	40	1/7,200, 1/72,000	36	28,584,000	99.2	98.6	208,800	0.7	0.7	14,400	0.1	0.1	28,807,200	99.4	64,800	0.2	122,400	0.4	—	—	28,994,400
WS 1054	68	8	1/300	13	3,900	44.8	3.9	4,800	55.2	4.7	—	—	—	8,700	8.6	11,100	11.0	69,000	68.5	12,000	11.9	100,800
WS 1053	55	2	1/150	15	1,500	38.5	9.3	2,400	61.5	14.8	—	—	—	3,900	24.1	3,600	22.2	4,650	28.7	4,050	25.0	16,200
WS 1052	35	10	1/600	16	4,800	15.7	2.5	25,800	84.3	13.6	—	—	—	30,600	16.1	13,800	7.3	130,200	68.4	15,600	8.2	190,200
WS 1051	19	12	1/600	19	67,500	27.0	15.5	183,000	73.0	41.9	—	—	—	250,800	57.4	15,600	3.6	41,400	9.5	130,200	29.5	438,000
WS 1050	8	12	1/300	27	103,500	60.4	49.4	67,500	39.4	32.3	300	0.2	0.1	171,300	81.8	2,400	1.1	24,000	11.5	11,700	5.6	209,400

enriched offshore community in the poorest sample. A tendency towards restriction of this group to the transition zone had also been apparent on several of the lines worked during the first survey.

Other main groups were very evenly distributed on the Möwe Point line during the second survey. The quantities of Metazoa were moderately high, and considerable quantities of Seston were recorded, suggesting that feeding and growth of the smaller plankton animals might be proceeding more uniformly and somewhat faster at this period than in the autumn.
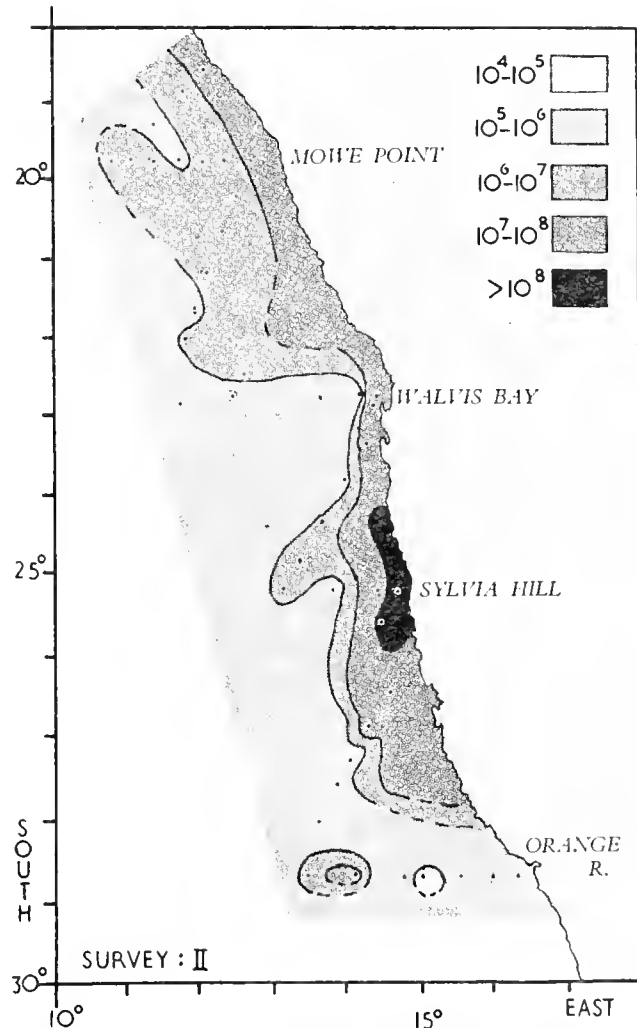
Fig. 65. Distribution of the microplankton, estimated totals per net haul, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

On the northern intermediate line (Fig. 67) similar conditions prevailed, indicating that the relative richness of offshore phytoplankton and general abundance of small zooplankton feeding voraciously were features distinguishing the samples collected during the second survey from the ones from corresponding first survey positions.

The figures for the Walvis Bay line (Fig. 68) show a rich diatom plankton right inshore and a secondary peak at station WS 1079. The work on this line was interrupted by a gale, so that some considerable time elapsed between the working of this and the preceding inshore stations. There is hydrological evidence (p. 188) supporting the view that surface-drift of inshore water during the interval led to this apparent anomaly. In other respects the features of the microplankton distribution offshore on this line during the second survey were similar to those found farther north: moderately high
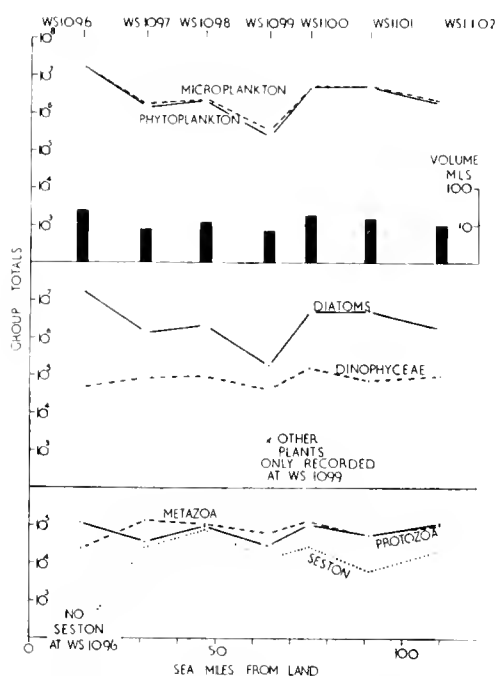
Fig. 66. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Möwe Point line, 9–11 October 1950. The histogram shows the settled volume of the catch in millimetres.
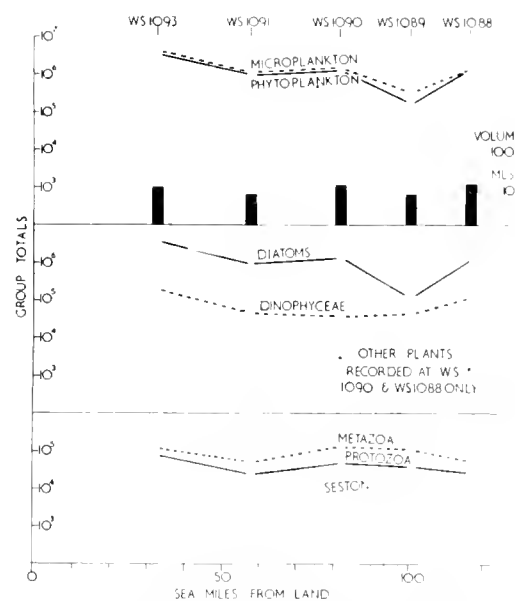
Fig. 67. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Northern Intermediate line, 8–9 October 1950.
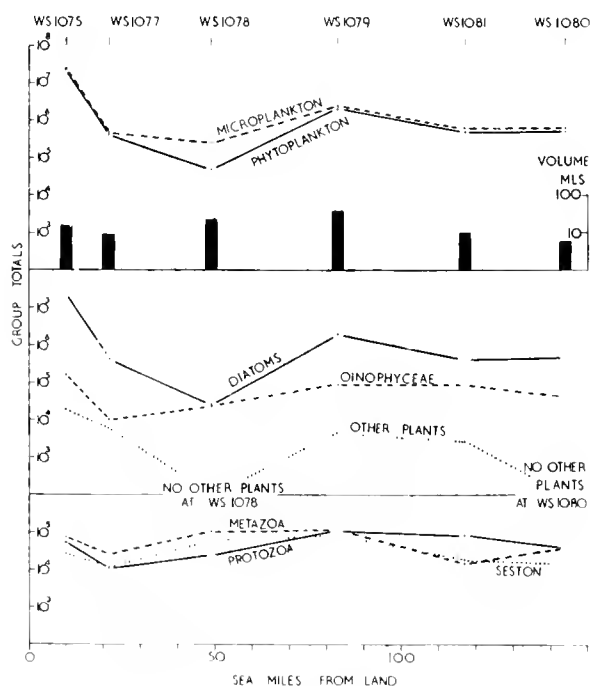
Fig. 68. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Walvis Bay line, 29 September–2 October 1950.
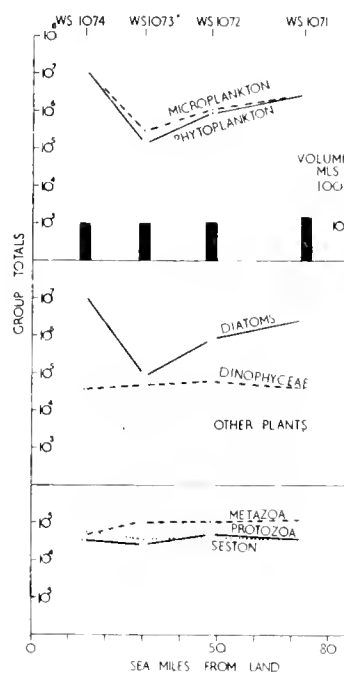
Fig. 69. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Middle Intermediate line, 28 September 1950.

values for Metazoa and Seston throughout, 'other plants' mainly in the transition zone and rather more diatoms, relatively, than had been found at the corresponding positions in autumn.

The group data for the mid-intermediate line show more profound differences from the conditions found there during the first survey. Then the diatom-rich coastal plankton had extended right out to the seaward end of the line (Figs. 61 and 65). During the second survey (Fig. 69) the rich coastal plankton with diatoms dominant was confined to the inshore station, the other groups were relatively more important throughout than they had been in autumn, and the secondary increase in diatoms towards the seaward end of the line was mainly due to offshore species. Conditions here and on the
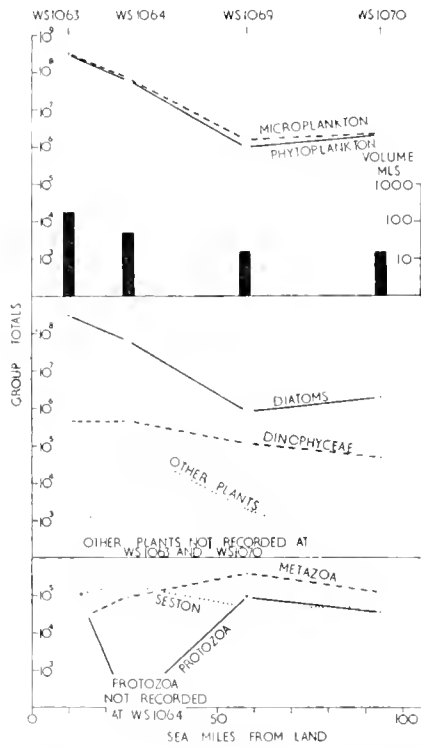
Fig. 70. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Sylvia Hill line, 21–24 September 1950.
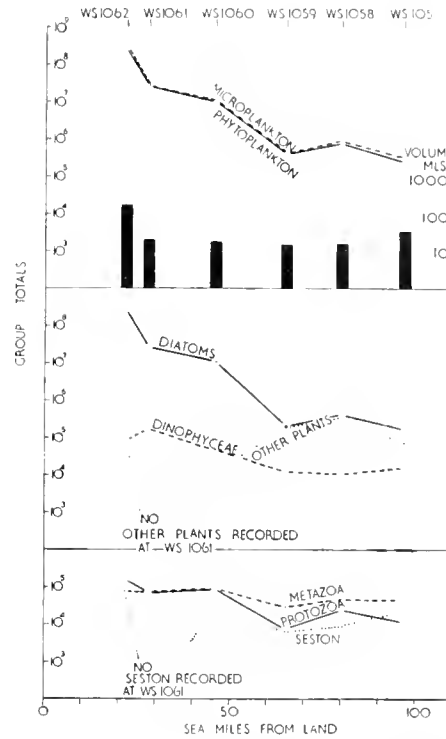
Fig. 71. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Southern Intermediate line, 24–25 September 1950.

adjacent lines both north and south displayed the general narrowing of the zone of rich coastal plankton that seemed characteristic of the second survey in its most extreme form.

The extremely rich diatom plankton found at the inshore station on the Sylvia Hill line (Fig. 70) showed clearly that, quite locally, the coastal population attained a density as great as that observed during the autumn, but proceeding seawards we again encountered the conditions met with farther north: a more rapid transition to relatively scanty offshore plankton, and greater relative abundance of Metazoa and Seston than had been observed there during the first survey.

A very similar distribution of the main groups was also evident on the southern intermediate line (Fig. 71) where the diatom population inshore was one of the richest sampled during either survey. 'Other plants', chiefly represented by isolated filaments and a few rafts of *Trichodesmium thiebautii*, attained their maximum numbers and greatest relative importance in the comparatively scanty offshore plankton on this line, but it should be emphasized that the species was not observed in anything approaching bloom-forming quantities.[1] Such blooms as we observed during the surveys were

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[1] It is one of the commonest and most widely distributed bloom-forming organisms throughout the warm and temperate regions of the South Atlantic.

due to diatoms, dinoflagellates and ciliate Protozoa, but it is quite probable that *Trichodesmium* may also form blooms within the area sometimes.

The conditions observed on the Orange river line during the second survey did not conform to the generalizations found to hold good for the rest of the area (Fig. 72). Here a diatom-rich plankton with both oceanic and neritic elements was found at the two offshore stations, and inshore there was an exceptionally poor phytoplankton with a high proportion of Metazoa and Seston. The hydrological data and qualitative plankton observations give some basis for the 'explanation', necessarily somewhat speculative, of this reversal of the usual pattern of quantitative distribution that has been attempted later (p. 245).
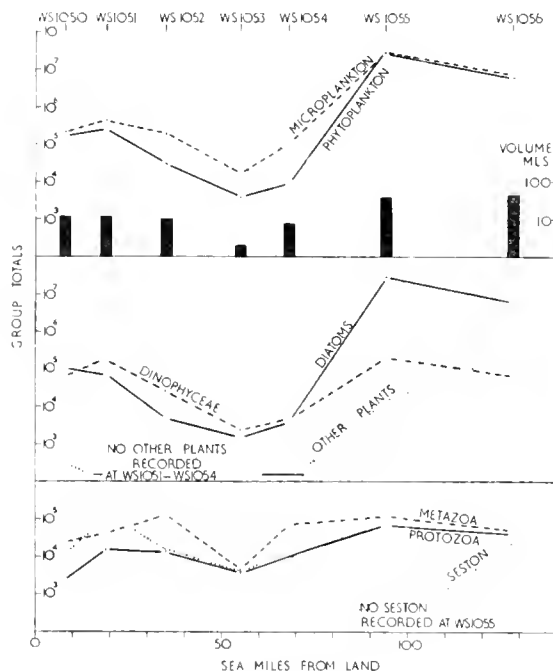
Fig. 72. Distribution of the main groups of microplankton, estimated totals per net haul, survey II, Orange river line, 21–24 September 1950.

DISTRIBUTION OF THE MAIN DIATOM GROUPS

First survey

The distribution of the main groups of diatoms, distinguished as described on p. 214, is summarized in Table 16. This shows the estimated total diatom numbers, estimated group totals, and relative percentages for each individual station. The stations are arrayed in order of the seven lines of observations as they were worked, from north to south (cf. Table 14).

As a further aid to description, the estimated group totals have been plotted on a logarithmic scale, in relation to the distance of each station from the coast (Figs. 73–76). In these figures the distance-scale reads seawards from the left of the page for each line, departing from the chronological sequence in order to secure uniformity of treatment in this respect.

In commenting on the group distribution, reference has been made to qualitative data not given here, because the group totals alone can be misleading where they unavoidably include species of widely differing ecological attributes. This involves some repetition later, the whole difficulty resulting from the impracticability of publishing the raw data in full.

On the Möwe Point line, the estimated diatom totals were small in comparison with those for the survey as a whole. They were highest inshore and showed a secondary peak at the shelf-edge,

Table 16. *First survey (autumn). Estimated total diatoms and numbers in the main diatom groups*

Station	Estimated total diatoms	Discineae Numbers	%	Biddulphiineae Numbers	%	Chaetoceraceae Numbers	%	Soleniineae Numbers	%	'Pennatae' Numbers	%
WS 964	73,124	47,060	64·4	nil	—	nil	—	19,548	26·7	6,516	8·9
WS 965	143,400	123,000	85·8	nil	—	nil	—	8,400	5·8	12,000	8·4
WS 966	363,750	26,250	7·2	nil	—	206,250	56·7	35,000	8·6	96,250	26·5
WS 967	1,634,250	61,750	3·8	30,000	1·8	1,030,000	63·0	32,500	2·0	480,000	29·4
WS 968	22,500	1,500	6·7	nil	—	2,250	10·0	12,000	53·2	6,750	30·0
WS 969	4,118,400	833,184	20·2	243,936	5·9	123,552	3·0	484,704	11·38	2,433,024	59·1
WS 970	1,382,500	108,500	7·8	112,000	8·2	172,000	12·4	810,000	58·6	180,000	13·0
WS 971	386,000	18,000	4·7	nil	—	8,000	2·1	334,000	58·6	26,000	6·7
WS 972	972,000	147,000	15·1	nil	—	33,000	3·4	231,000	23·8	516,000	57·7
WS 973	1,010,000	276,000	27·3	nil	—	nil	—	418,000	41·4	316,000	31·3
WS 974	314,000	156,000	49·7	nil	—	nil	—	46,000	14·6	112,000	35·7
WS 975	202,000	24,000	11·9	nil	—	34,000	16·8	18,000	8·9	126,000	62·4
WS 976	282,000	20,000	7·1	nil	—	6,000	2·1	58,000	20·6	198,000	70·2
WS 977	212,000	20,000	9·4	nil	—	64,000	30·2	62,000	29·3	66,000	31·1
WS 978	816,000	21,600	2·6	nil	—	552,000	67·6	74,400	9·2	68,000	20·6
WS 979	98,328,000	2,000,000	2·0	80,000	0·1	93,888,000	95·5	32,000	<0·1	2,328,000	2·4
WS 980	45,344,000	1,936,000	4·3	3,328,000	6·9	22,080,000	49·1	264,000	0·6	17,736,000	39·1
WS 981	9,987,300	2,185,200	21·9	194,400	2·0	2,570,400	25·7	69,300	0·7	4,968,000	49·7
WS 982	74,070,000	1,302,000	1·8	384,000	0·5	59,580,000	80·4	1,488,000	2·0	11,316,000	15·3
WS 983	40,180,800	2,305,200	5·7	648,000	1·6	36,792,000	91·6	72,000	0·2	363,600	0·9
WS 984	69,432,000	168,000	0·2	nil	—	67,968,000	97·9	336,000	0·5	960,000	1·4
WS 985	27,477,000	396,000	1·4	nil	—	25,992,000	94·6	45,000	0·2	1,044,000	3·8
WS 986	97,300	4,300	4·4	2,500	2·6	34,000	34·9	10,000	10·3	46,500	47·8
WS 987	11,400	3,600	31·5	nil	—	6,900	60·5	900	8·0	nil	—
WS 988	270,450,000	9,720,000	3·6	7,470,000	2·7	208,170,000	77·0	4,005,000	1·5	41,085,000	15·2
WS 989	158,508,000	8,649,000	5·5	4,329,000	2·7	118,872,000	75·0	1,512,000	0·9	25,146,000	15·9
WS 990	74,006,400	4,147,200	5·6	105,600	0·2	56,448,000	76·3	614,400	0·8	12,691,200	17·1
WS 991	258,300,000	nil	—	nil	—	243,450,000	94·3	nil	—	14,850,000	5·7
WS 992	50,692,800	100,800	0·2	96,000	0·2	45,024,000	88·8	nil	—	5,472,000	10·8
WS 993	19,800	4,200	21·2	nil	—	9,300	47·0	4,500	22·7	1,800	9·1
WS 994	16,800	1,800	10·7	nil	—	5,100	30·4	2,400	14·3	7,500	44·6
WS 995	12,300	1,800	14·6	nil	—	8,400	68·3	nil	—	2,100	17·1
WS 996	16,000	3,000	18·8	nil	—	2,000	12·5	4,000	25·0	7,000	43·7
WS 997	13,800	4,500	32·6	nil	—	300	2·2	2,400	17·4	6,600	47·8
WS 998	3,000	750	25·0	nil	—	500	16·7	nil	—	1,750	58·3
WS 999	1,200	nil	—	nil	—	200	16·7	400	33·3	600	50·3
WS 1000	42,300	300	0·7	nil	—	41,400	97·9	600	1·4	nil	—
WS 1001	7,758,000	nil	—	nil	—	7,434,000	95·8	nil	—	324,000	4·2
WS 1002	43,710,000	nil	—	nil	—	38,006,000	87·0	nil	—	5,704,000	13·0

diminishing to characteristically small oceanic values offshore. There was a marked minimum between the two peaks, believed to be due to intrusion of offshore water.

Considering the groups severally, it can be seen that the Discineae reached their greatest numbers in the richer inshore water. Here the neritic *Stephanopyxis* was dominant. The greatest relative importance of the group was attained at the poorer offshore stations, however, where the essentially oceanic *Planktoniella sol* accounted for most of the group-total.

Biddulphiineae were observed only at the two inshore stations, and at the secondary peak station near the shelf-edge. The neritic species *Eucampia zoodiacus* was the only one seen in the fractions counted, and the group was of little relative importance.

Chaetoceros species were unusually scanty close inshore, but predominated at the shelf-edge peak station. The group was not seen at all at the two offshore stations though these were re-examined carefully.

Soleniineae were abundant close inshore, present elsewhere in very moderate numbers, becoming of some relative importance only in the very small minimal haul, and again at the outer end of the line. *Leptocylindrus danicus*, one of the few neritic species in this essentially holoplanktonic group, was mainly responsible for the inshore maximum. Various *Rhizosolenia* species, among the most cosmopolitan of all plankton diatoms, were present at the minimal station; while right offshore the oceanic species *Rhizosolenia simplex* was the dominant form.

'Pennatae' formed an unusually high proportion of the total diatom count at the inshore peak station and were second only to Chaetoceros among the group totals at the shelf-edge peak. The small 'reversionary plankton forms' *Nitzschia* spp. and *Asterionella japonica* were chiefly responsible, with a considerable proportion of the larger *Thalassiothrix longissima* at the shelf-edge. The latter usually showed a more oceanic distribution than other members of the group in these surveys.

Fig. 73. Estimated total diatoms, and diatom group totals, survey I. A. Möwe Point line, 4–5 March 1950.
B. Northern Intermediate line, 5 March 1950.

On the northern intermediate line, the estimated diatom totals were very moderate throughout, with a slight maximum at the second and third stations seaward, diminishing to the outer end of the line.

From the group figures it appears that Discineae were relatively somewhat more important in the small catches here than over the survey area generally. The panthalassic species *Thalassiosira excentrica* and *Planktoniella sol* (oceanic) were both among the dominants at the three slightly richer stations at the middle of the line. This may have been due to the mixing conditions thought to have obtained within the '*Goniaulax*-patch' (see p. 251).

Biddulphiineae were not observed in the routine analyses on this line and species of Chaetoceros were present in small number at the two inshore stations only. A majority of this group proved to be mainly neritic throughout the survey, but on the other lines they were nearly always dominant inshore; not the most poorly represented group, as here. Soleniineae were dominant inshore and at the peak station, represented mainly by panthalassic cosmopolitan species such as *Rhizosolenia hebetata* and *R. alata*; the falling off in relative importance of this group towards the seaward end of the line was an unusual feature thought to be bound up with the mixing conditions referred to above.

On this northern intermediate line the 'Pennatae' were the most important single group numerically, with the minute *Nitzschia delicatissima* the most important individual species, joined by the large

Thalassiothrix longissima at the seaward end of the line (one of the few details in which this series approached a norm for the area as a whole!).

On the Walvis Bay line (Fig. 74) the estimated diatom totals reached high values at the three inshore stations, with a sharp decline beyond the shelf-edge, levelling out to moderate amounts at the two oceanic offshore stations. The high inshore values proved typical of the main upwelling region on most of the lines worked throughout both surveys, as can be seen from the subsequent diagrams.

Discineae were present in fair numbers inshore, represented mainly by *Stephanopyxis turris* and *Thalassiosira subtilis*, the one definitely a neritic species, the other panthalassic. Offshore the numbers declined, at first in parallel with the estimated diatom totals, levelling at the two outer stations to give a slight secondary increase in relative importance. This was due mainly to the species *Thalassiosira*
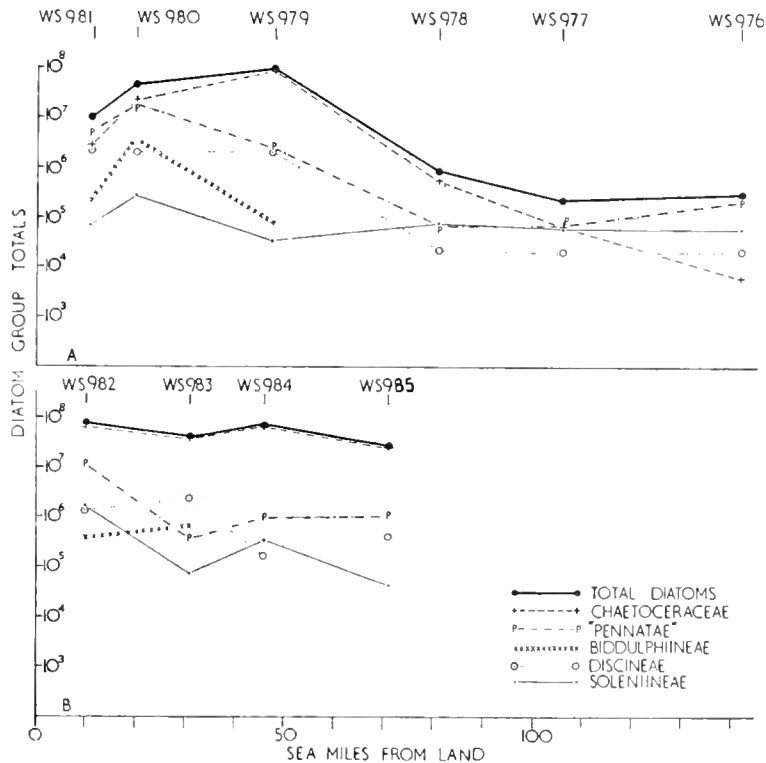
Fig. 74. Estimated total diatoms, and diatom group totals, survey I. A. Walvis Bay line, 6–8 March 1950.
B. Middle Intermediate line, 9–10 March 1950.

excentrica, with lesser numbers of *Planktoniella sol*. Biddulphiineae were present inshore and of considerable importance at station WS 980, but were not observed seawards of the peak station WS 979. The group was represented here entirely by *Eucampia zoodiacus*, as on the Möwe Point line.

Chaetoceros was by far the most important group over the Walvis Bay line as a whole. It was strongly dominant at the two richest inshore stations, where a profusion of neritic species were present, and at the first of the poorer stations, seawards. There, however, the single 'relatively oceanic' species *Chaetoceros convolutum* alone accounted for most of the group total. Still further offshore the group dwindled rapidly, both in estimated numbers and in relative importance.

Soleniineae were present at all stations on the line in consistently small numbers, becoming relatively important in the poorest offshore plankton. Cosmopolitan *Rhizosolenia* spp. predominated throughout, accompanied at one inshore station, where the group total was highest, by the mainly neritic *Dactyliosolen mediterraneus*.

'Pennatae' were an important group on this line, especially at the innermost and outermost stations

where they predominated. Even at the intervening stations they ranked second only to the chaeto-
cerids. The unavoidably heterogeneous nature of the group, however, was very evident. Whereas
inshore the strongly neritic species *Fragilaria karsteni* predominated, along with *Asterionella japonica*,
it was the oceanic *Thalassiothrix longissima* and panthalassic *Nitzschia delicatissima* that accounted for
nearly all of the group totals farther out.

The mid-intermediate line proved too short to extend beyond the rich coastal diatom zone. The
estimated diatom totals were high throughout and very closely paralleled by the group-totals for the
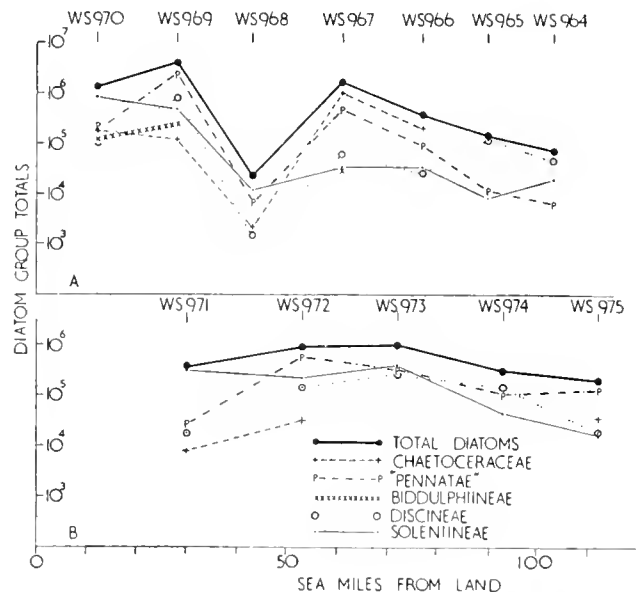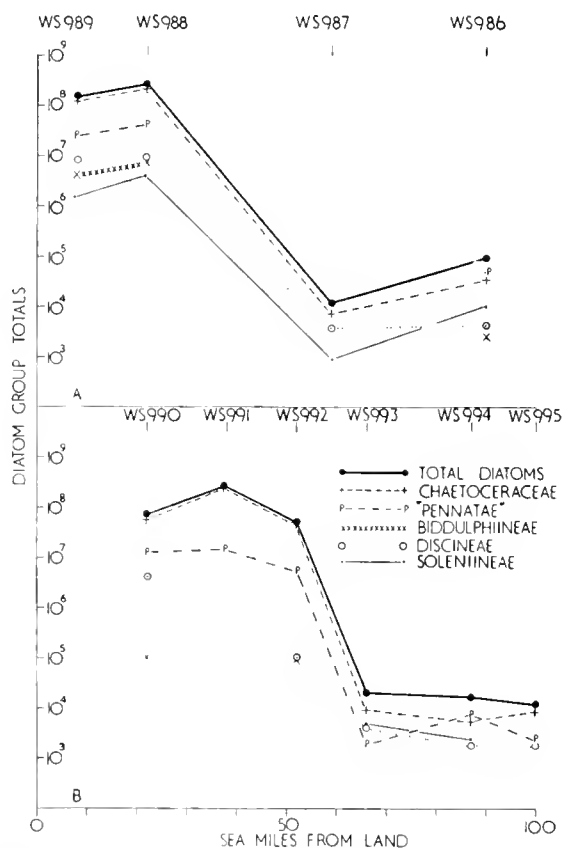

Fig. 75. Estimated total diatoms, and diatom group totals, survey I. A. Sylvia Hill line, 10–11 March 1950.
B. Southern Intermediate line, 11–12 March 1950.

predominating chaetocerids. The other groups clearly fulfilled a minor role, much on the same level,
with 'Pennatae' of some consequence inshore. Apart from the profusion of neritic *Chaetoceros*
species, at least ten in number, the species of most importance were:

Among the Discineae, inshore, *Stephanopyxis turris* diminishing rapidly as one proceeded seawards;
and *Thalassiosira subtilis*, which reached its highest numbers and relative importance at station
WS 983.

Among the Biddulphiineae, *Eucampia zoodiacus* at the two inshore stations only.

Among the Soleniineae, *Dactyliosolen mediterraneus* and much lesser numbers of the more cosmo-
politan *Rhizosolenia* spp. farther offshore.

Among the 'Pennatae', *Fragilaria Karsteni* and *Asterionella japonica* inshore with *Thalassiothrix
longissima* at station WS 984.

On the Sylvia Hill and southern intermediate lines, diatom distribution followed an essentially
similar pattern. Very high estimated totals were recorded inshore, with an abrupt decrease near the
shelf-edge some 60 sea-miles from the land, and a levelling out to very low values towards the sea-

ward ends of each series of observations. Chaetocerids were by far the most important group, as can be seen from the way in which their group-totals follow closely in parallel with the figures for total diatoms. Inshore they were represented by the usual rich variety of species, mainly neritic but some with panthalassic tendencies. Offshore there was some apparent overspill of the most abundant inshore forms, but the more definitely oceanic members of the genus, such as *Chaetoceros convolutum* and *C. peruvianum*, were relatively much more important in the very poor phytoplankton met with there.

The estimated totals for other groups was also greatest inshore, but the relative importance of those with offshore representatives was much greater near the shelf-edge and beyond.

The Discineae were represented mainly by *Thalassiosira* spp. Of these *T. hyalinum*, *T. rotula* and the panthalassic *T. subtilis* were commonest inshore; *T. excentrica* and *T. subtilis* (again!) offshore. The oceanic *Planktoniella sol* was of some relative importance in one extremely small sample from near the outer end of the southern intermediate line.
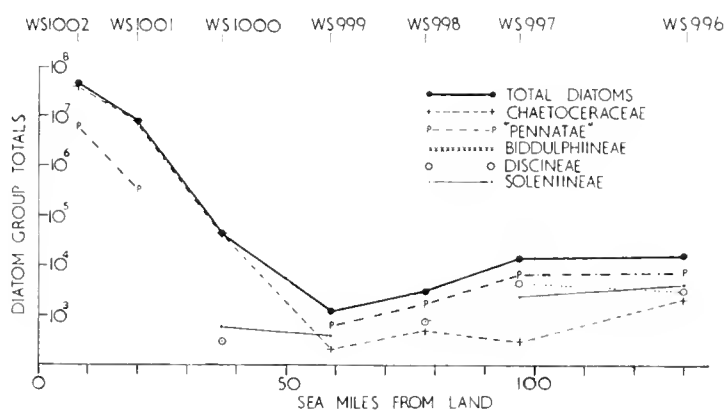
Fig. 76. Estimated total diatoms, and diatom group totals, survey I, Orange river line, 12–14 March 1950.

The Biddulphiineae were almost entirely confined to the inshore stations on both series, though *Eucampia zoodiacus* was recorded in very small numbers from station WS 986, at the seaward end of the Sylvia Hill line. This same species accounted for most of the inshore totals for the group, as we had found farther north at this season, but here there was a small proportion of *Cerataulina pelagica* in addition.

Soleniineae formed only a small proportion of these samples. The higher numbers at three inshore stations were due to the mainly neritic species *Dactyliosolen mediterraneus* and *Leptocylindrus danicus*. The very small totals for this group at offshore stations show that it was of some slight relative importance there, but only because of the prevailing poverty of the offshore phytoplankton. The offshore species included *Bacteriastrum hyalinum*, the more cosmopolitan *Rhizosolenia* spp. and *R. simplex*.

The 'Pennatae' were more heavily outnumbered by the dominant chaetocerids at the inshore stations of these two lines than they had been farther north, but still ranked second among the diatom groups. The dominant inshore species—*Fragilaria karsteni*, *Asterionella japonica* and *Nitzschia seriata*—were the same as those recorded on the two previous lines. Offshore small numbers of *Nitzschia delicatissima*, *N. seriata* and *Thalassiothrix longissima* accounted for most of the group totals, together with *Fragilaria granulata* at station WS 994. This species was recorded only at this one station during the first survey, but much more frequently and abundantly during the second, when it showed a consistently offshore distribution. The very small totals of 'Pennatae' recorded at stations WS 986 and 994 just suffice to indicate greater relative importance than that of the chaetocerids, so clearly dominant at all the other stations of the Sylvia Hill and southern intermediate lines.

Although the very great difference in quantity between the rich diatoms inshore and the impoverished phytoplankton population farther out is well shown by these two series of observations, the qualitative distinctions are less clear than they seemed to be on other lines worked during the first survey. This is believed to be due to the wide tolerance of the more panthalassic species of *Chaetoceros*, *Nitzschia* and *Thalassiosira*. Prolongation of the lines seaward would almost certainly have demonstrated their replacement as dominants by more exclusively oceanic species, but this desideratum could not be foreseen in planning the surveys. 'Ideal' coverage can never be wholly attainable in such work, and had we extended these two series, practical considerations of steaming time, fuel consumption and water supply must have enforced a corresponding curtailment of the rest of the ship's programme.

The inshore zone of rich diatom phytoplankton was narrower on the Orange river line (Fig. 76) although the shelf is wider there, and diatoms were exceptionally scanty for a considerable distance seaward. Even at the two stations right out beyond the shelf-edge the catches were still very small. Peculiar local conditions must have obtained here, for the rich zooplankton and abundance of Seston indicate heavy grazing of what must have been a very much richer standing crop of plants not long before. Further deviation from the conditions prevailing farther north were indicated by the presence of essentially neritic species along with the oceanic ones at the stations farthest from land.

Even so, apart from the narrowing of the rich coastal belt and extreme poverty of the outer stations on the shelf, the group distribution of diatoms on this line still shows *some* of the main features observed farther north. Thus most of the chaetocerids so completely dominant inshore were neritic ones, although the panthalassic species *Chaetoceros convolutum* was present in greater proportion than was usual inshore elsewhere. The decline in relative importance of this group at the impoverished offshore stations, with correspondingly increased proportions of Discineae, Soleniineae and 'Pennatae' there, is well shown in Fig. 76.

Specific data for the groups other than *Chaetoceros* show that the panthalassic *Thalassiosira subtilis* and oceanic *Planktoniella sol* among the Discineae and *Thalassiothrix longissima* among the 'Pennatae' were relatively more important offshore as in the other more normal series.

Second survey

Similar treatment of the data from the Möwe Point line on the second survey shows that at that season, although the inshore station was still the richest by far, the diatom totals diminished rapidly as the ship proceeded offshore. A minimum was reached at station WS 1099 near the edge of the shelf and there was then a considerable secondary rise in estimated totals at the three offshore stations (Table 17 and Fig. 77).

Totals for each of the four main diatom groups present[1] varied roughly in parallel with those for total diatoms, but whereas the numbers and the proportion of *Chaetoceros* and 'Pennatae' were greatest inshore, there were many more Soleniineae present at the outer stations. These outer stations were somewhat less well defined qualitatively than those on some of the more southerly series at group level, since they still contained a moderately high proportion of Discineae and *Chaetoceros*, both groups containing a majority of inshore species. The more detailed data seem to show up their distinction fairly clearly, though there was evidently more tendency towards offshore transport in the turbulent conditions prevailing than had been observed during the autumn survey.

Among the Discineae the inshore maximum was due mainly to *Stephanopyxis turris* and *Thalassiosira* spp. Though the secondary rise in numbers of the group at the offshore stations included some of these two categories, *Stephanopyxis* there formed a much smaller proportion of the totals, *Thalas-*

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[1] Biddulphiineae were not observed on this line.

Table 17. *Second survey (spring). Estimated total diatoms and numbers in the main diatom groups*

Station	Estimated total diatoms	Discineae Numbers	%	Biddulphiineae Numbers	%	Chaetoceraceae Numbers	%	Soleniineae Numbers	%	'Pennatae' Numbers	%
WS 1102	1,734,000	42,000	2·4	nil	—	606,000	34·9	729,000	42·1	357,000	20·6
WS 1101	5,208,000	162,000	3·1	nil	—	1,632,000	31·3	2,640,000	50·7	774,000	14·9
WS 1100	4,968,000	189,000	3·8	nil	—	792,000	15·9	3,609,000	72·7	378,000	7·6
WS 1099	185,400	9,000	4·9	nil	—	28,800	15·5	49,500	26·7	98,100	52·9
WS 1098	2,082,000	90,000	4·3	nil	—	930,000	44·7	300,000	14·4	762,000	36·6
WS 1097	1,398,000	132,000	9·4	nil	—	531,000	38·0	105,000	7·5	630,000	45·1
WS 1096	19,320,000	3,072,000	15·9	nil	—	11,064,000	57·3	936,000	4·8	4,248,000	22·0
WS 1093	3,618,400	489,600	13·5	nil	—	2,091,600	57·8	126,000	3·5	911,200	25·2
WS 1091	969,300	51,300	5·3	nil	—	221,400	22·8	518,400	53·5	178,200	18·4
WS 1090	1,317,000	81,000	6·2	nil	—	492,000	37·4	609,000	46·2	135,000	10·2
WS 1089	117,000	16,200	13·8	nil	—	9,900	8·5	85,500	73·1	5,400	4·6
WS 1088	1,159,500	1,500	0·1	nil	—	48,000	4·1	1,101,000	95·0	9,000	0·8
WS 1080	483,300	18,900	3·9	nil	—	8,100	1·7	405,000	83·8	51,300	10·6
WS 1081	405,000	10,800	2·7	nil	—	24,300	6·0	256,500	63·3	113,400	28·0
WS 1079	1,962,000	58,500	3·0	nil	—	198,000	10·1	1,206,000	61·4	499,500	25·5
WS 1078	25,500	7,500	29·4	nil	—	nil	—	nil	—	18,000	70·6
WS 1077	402,600	133,800	33·2	8,400	2·1	87,600	21·8	nil	—	172,800	42·9
WS 1075	22,923,000	576,000	2·5	nil	—	11,061,000	48·3	45,000	0·2	11,241,000	49·0
WS 1074	11,835,000	315,000	2·7	6,000	<0·1	1,326,000	11·2	6,000	<0·1	10,182,000	86·0
WS 1073	87,000	19,500	22·4	nil	—	52,500	60·3	3,000	3·5	12,000	13·8
WS 1072	820,800	79,200	9·6	nil	—	168,000	20·5	393,600	48·0	180,000	21·9
WS 1071	2,694,000	39,000	1·4	nil	—	195,000	7·2	1,698,000	63·1	762,000	28·3
WS 1070	1,941,600	52,800	2·7	nil	—	734,400	37·8	508,800	26·2	645,600	33·3
WS 1069	840,600	882,00	10·5	nil	—	654,000	77·8	22,800	2·7	75,600	9·0
WS 1064	67,950,000	630,000	0·9	270,000	0·4	64,800,000	95·4	180,000	0·3	2,070,000	3·0
WS 1063	312,300,000	1,200,000	0·4	30,000	<0·01	296,100,000	94·8	210,000	<0·1	14,760,000	4·7
WS 1062	258,680,000	1,000,000	0·4	480,000	0·2	236,800,000	91·6	nil	—	20,400,000	7·8
WS 1061	27,264,000	2,136,000	7·8	24,000	0·1	19,440,000	71·3	nil	—	5,664,000	20·8
WS 1060	10,740,000	252,000	2·3	nil	—	6,816,000	63·5	nil	—	3,672,000	34·2
WS 1059	199,800	36,000	18·0	nil	—	19,800	9·9	19,200	9·6	124,800	62·3
WS 1058	416,400	44,400	10·7	3,600	0·9	84,000	20·2	36,000	8·6	248,400	59·6
WS 1057	161,200	72,540	45·0	nil	—	14,260	8·8	11,160	7·0	63,240	39·2
WS 1056	6,375,600	171,600	2·7	39,600	0·6	4,422,000	69·4	198,000	3·1	1,544,400	24·2
WS 1055	28,584,000	1,281,600	4·5	nil	—	25,488,000	89·2	72,000	0·2	1,742,400	6·1
WS 1054	3,900	2,100	53·8	nil	—	nil	—	nil	—	1,800	46·2
WS 1053	1,500	1,050	70·0	nil	—	150	10·0	nil	—	300	20·0
WS 1052	4,800	3,000	62·5	nil	—	nil	—	nil	—	1,800	37·5
WS 1051	67,800	24,000	35·4	nil	—	38,400	56·6	600	0·9	4,800	7·1
WS 1050	103,500	39,600	38·3	nil	—	55,200	53·3	nil	—	8,700	8·4

siosira showed specific differences, and there was a very marked increase in the typically oceanic *Planktoniella sol* (absent inshore) from station WS 1099 seawards.

Some of the dominant coastal chaetocerids persisted (in reduced numbers) to the outer end of the line, but again more typically offshore forms such as *C. convolutum* and *C. lorenzianum* showed marked increase in relative importance from station WS 1099 seawards. Similar specific differences were shown within the two other groups also: Inshore *Rhizosolenia setigera* and *Leptocylindrus danicus* were the most important solenoids, while offshore *Rhizosolenia styliformis* and *Dactyliosolen mediterraneus* were the most abundant of all the diatoms at this time. *Fragilaria karsteni* and *Asterionella japonica* were among the dominant 'Pennatae' inshore. The former was not seen more than 30 sea-miles from land, and though *Asterionella* was found farther out it was present only in relatively small numbers there. The cosmopolitan *Nitzschia seriata* was observed in both localities, but offshore it appeared that *N. delicatissima* was the most numerous species of the group at this season.

The results from the northern intermediate line showed essentially the same features as those observed off Möwe Point, most of them even more definitely (Fig. 77). It is true that *Fragilaria karsteni* was not present among the 'Pennatae' at the inshore station, but this was 30 miles from the land, and from all our other observations the species seemed to be the most strongly neritic in habit of all the important plankton forms in this area. The solenoid community, with some few of the more oceanic *Chaetoceros* spp. was even more completely dominant offshore, where the line extended into a region where almost all the microplankton was essentially oceanic in character. At station WS 1088, no less than 94% of the diatoms was made up of the cosmopolitan *Rhizosolenia* spp. *R. styliformis*, *R. hebetata* and *R. imbricata*.
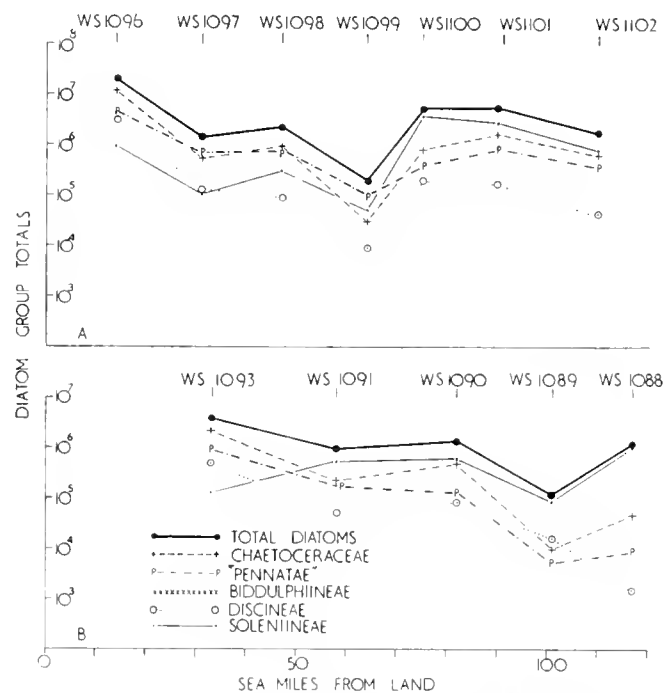
Fig. 77. Estimated total diatoms and diatom group totals, survey II. A. Möwe Point line, 9–11 October 1950. B. Northern Intermediate line, 8–9 October 1950.

The dominance of this solenoid community at offshore stations persisted in very marked degree at the outer end of the Walvis Bay line, where, however, there was a larger proportion of *Thalassiothrix longissima*, perhaps the most oceanic of the 'Pennatae', among the small fraction of the total not accounted for by the solenoids. Indeed it would appear that with minor modifications the solenoids predominated in the offshore plankton from about the middle of the area to the northern limit of our serial observations at the time of this second survey (cf. Table 17, Figs. 76–8).

The inshore stations on both the Walvis Bay and mid-intermediate lines also displayed common features that differed markedly from those observed in autumn. In spring the rich coastal flora of *Chaetoceros* spp., with *Asterionella* and *Fragilaria karsteni* among the 'Pennatae', etc., was confined to the innermost stations, with an abrupt diminution seawards *before* the shelf-edge was reached. There was thus a pronounced narrowing of the rich coastal belt here in spring, where it had been wide, and fanned out seaward to the shelf-edge on the Walvis Bay line, during the first (autumnal) survey (cf. Fig. 57 and Fig. 65). The spring results resembled more the extreme contrast within a relatively short distance out from the coast, that had been shown on the Sylvia Hill line, immediately to the southward, in autumn. The distributional pattern is consistent with the active upwelling which was demonstrated by the hydrological results from this region. Within the upwelling water, the larger

concentrations of phytoplankton were found at the stations nearest to the coast, and there was a rapid decrease seawards before even the shelf-edge was reached. On the occasions where the stations extended far enough from the coast, a secondary increase in the phytoplankton is evident—the abundance beyond the shelf-edge was greater than on the first survey. The population in this secondary increase included some oceanic forms among its dominants and it seems probable that it was associated with the divergence of oceanic water beyond the shelf-edge, which was postulated in the interpretation of the mechanism of upwelling (p. 188, Fig. 37).

Turning to conditions observed on the Sylvia Hill line itself during the second survey (Fig. 79) it can be seen that although the falling-off seawards was pronounced, diatom members were still very
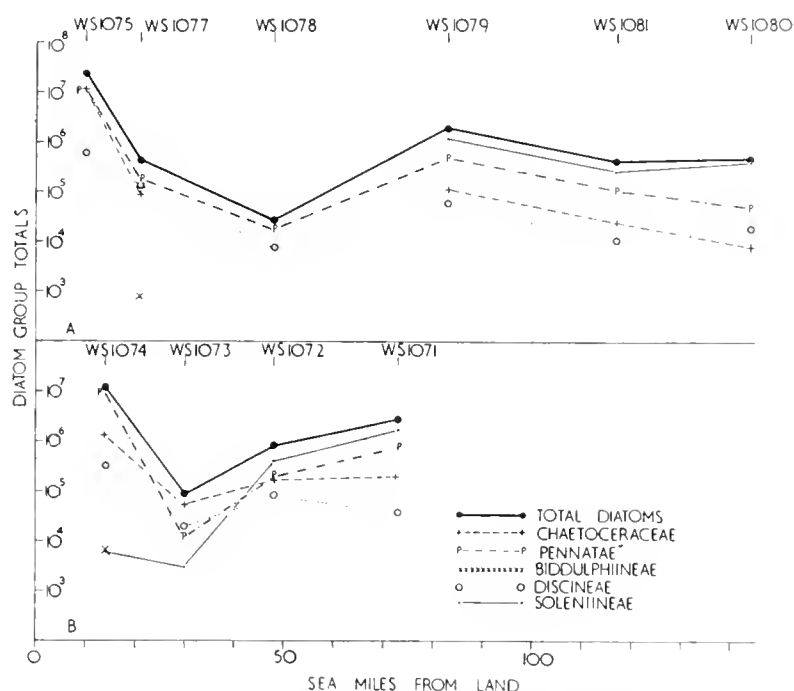
Fig. 78. Estimated total diatoms and diatom group totals, survey II. A. Walvis Bay line, 29 September–2 October 1950. B. Middle Intermediate line, 28 September 1950.

high at the second station seawards, with coastal chaetocerids and 'Pennatae' still strongly dominant. While the neritic Biddulphiineae were observed at the inshore station only, as was to be expected, members of the other two groups persisted right to the outer end of this comparatively short line, and it was only at the outermost station that the oceanic solenoids became equally important. This distribution resembled that seen on the mid-intermediate line (that next to the N. in the series) during the first survey.

On the southern intermediate line, the falling-off in quantity from the exceptionally rich inshore station was steep, but the succeeding stations seawards were still quite rich and showed a typical coastal flora extending fully 50 sea-miles from the coast. It seems probable that here again the inshore stations were characteristic of the active upwelling shown on the Sylvia Hill line. The sharp fall in abundance from station WS 1060 to station WS 1059, and the persistence at the latter station and those towards the seaward end of the line of a scanty oceanic type of plankton, was correlated with the pronounced intrusion of oceanic water to the north of the Orange river line, illustrated by the surface-temperature pattern (Fig. 7b).

The detailed figures for the southern intermediate line in spring show some minor anomalies at group level that require comment. At the outer oceanic station Discineae and 'Pennatae', both

groups containing a majority of inshore species, were relatively important. The individual counts show, however, that the oceanic species *Planktoniella sol* accounted for most of these Discoidae, and the typically offshore species *Thalassiothrix longissima* and *Fragilaria granulata* were prominent among the 'Pennatae', though in that group panthalassic *Nitzschia* spp. were also numerous. It was here that
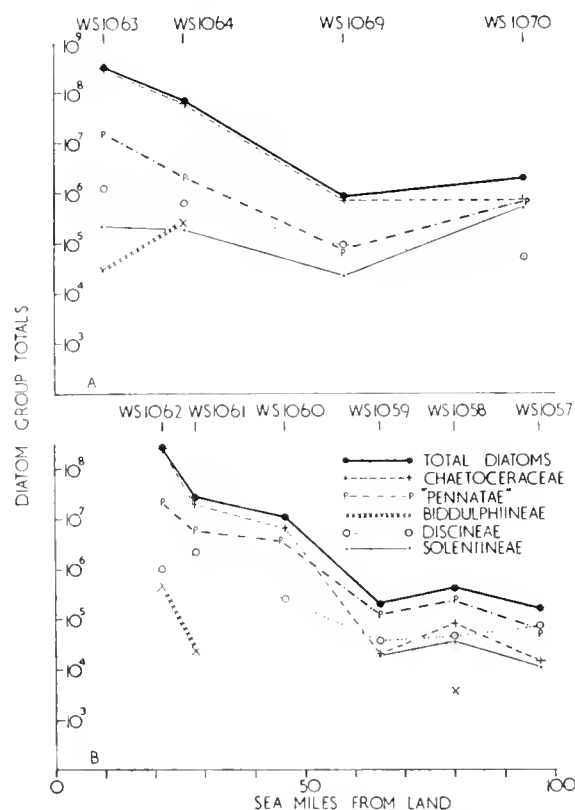
Fig. 79. Estimated total diatoms and diatom group totals, survey II. A. Sylvia Hill line, 25–27 September 1950.
B. Southern Intermediate line, 24–25 September 1950.
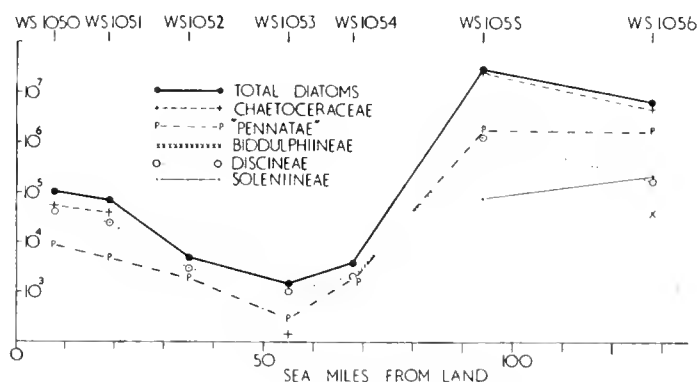
Fig. 80. Estimated total diatoms and diatom group totals, survey II, Orange river line, 21–24 September 1950.

relatively large numbers of *Trichodesmium thiebautii*, the filamentous, sometimes colonial blue-green alga most important among the few 'other plants' in these samples, were met with.

Finally, the Orange river line showed an extraordinary reversal of the conditions observed during the first survey, the two diatom-rich stations now being found far beyond the projecting shelf-edge at the outer end of the line. Further, they showed a most extraordinary admixture of species. Though oceanic forms such as *Chaetoceros atlanticum*, *C. peruvianum* and *Planktoniella sol* were among the dominants, the essentially coastal *Chaetoceros compressum* was abundant at station WS 1055. In the

absence of further serial observations to the southward, we can but speculate as to the reasons for this reversal of a feature that remained clear throughout the eleven other series of both surveys. We have seen from the hydrological sections that active upwelling was very pronounced on this line of stations. The stations on the continental shelf lay within the very recently upwelled water, perhaps too recent for extensive plankton production to have got under weigh. The two rich stations were beyond the edge, and may be comparable with those showing secondary offshore increase in phytoplankton on the more northerly series of observations.

Fig. 81. Distribution of *Chaetoceros*, survey I, March 1950. (Station numbers are shown in Fig. 1.)
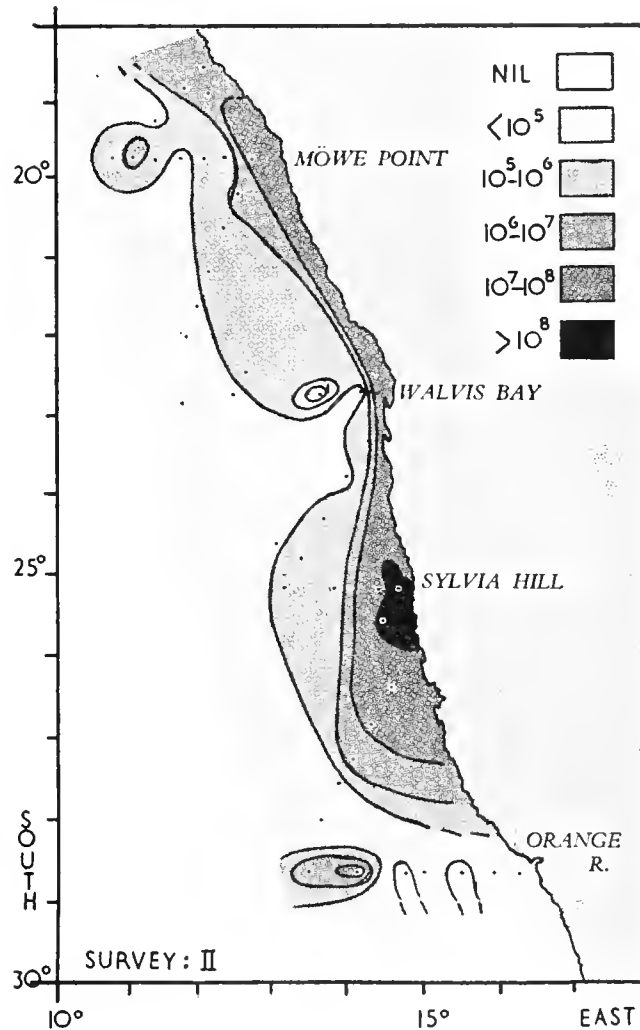
Fig. 82. Distribution of *Chaetoceros*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

SPECIAL DISTRIBUTIONAL FEATURES

It is hoped that the following figures are fairly illustrative of the main distributional trends, summarizing the features described in discussing group distributions, and giving examples of the most marked divergences from typical group pattern shown by certain individual species. Most of them are based upon estimated numbers per net haul, contoured logarithmically. Percentage of total diatoms has been used as the criterion for certain categories whose great relative importance in the scanty offshore plankton could not be shown by consideration of their numbers alone. This need arises from their cosmopolitan tendencies permitting them to attain equal or even greater abundance

farther inshore, without, however, forming any significant proportion of the vastly richer vegetation present there (cf. Figs. 93–5).

Figs. 81 and 82 show the outstanding importance of the group Chaetoceraceae in the rich coastal waters during both the seasons studied, and the relative narrowing of that zone in spring as compared with autumn (1st survey). Comparison with Figs. 57 and 65 shows how large a proportion of the total microplankton observed inshore was composed of the members of this one group of diatoms.
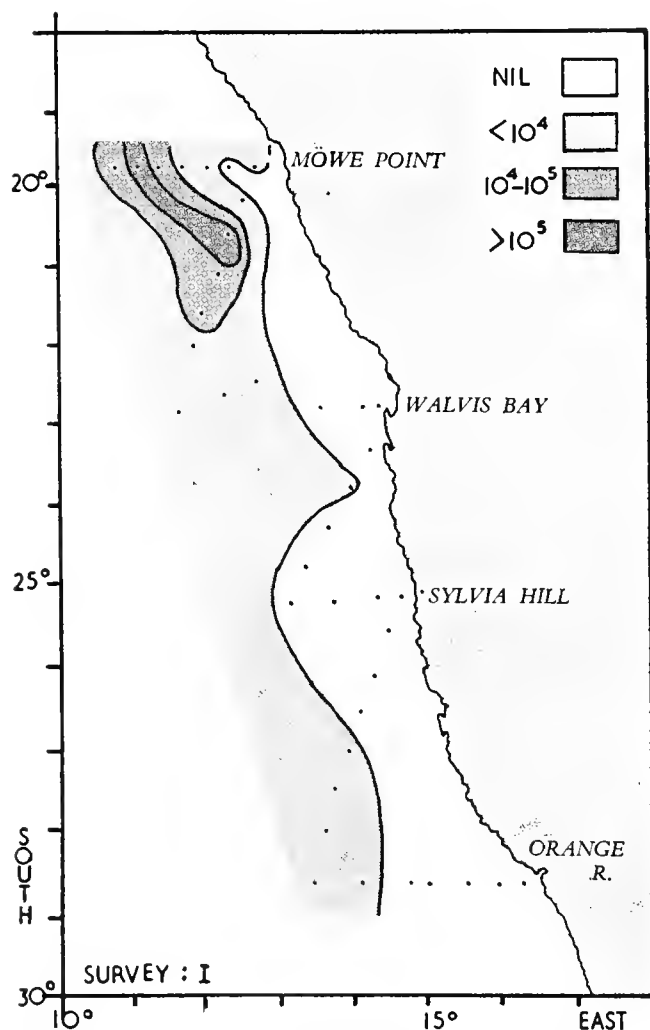
Fig. 83. Distribution of *Planktoniella*, survey I, March 1950. (Station numbers are shown in Fig. 1.)
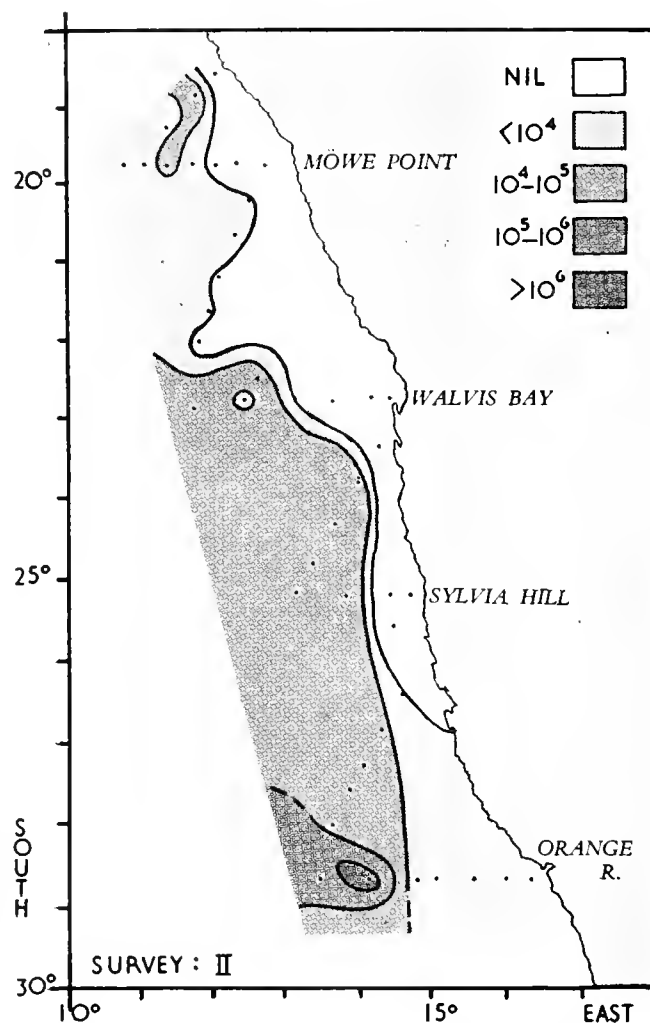
Fig. 84. Distribution of *Planktoniella*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

The distribution of the one discoid species found to be most numerous in the scanty offshore phytoplankton—*Planktoniella sol*—is shown in Figs. 83 and 84. The finger-like extensions towards the coast shown near the northern limits of the rich coastal upwelling area seem fairly indicative of actual intrusions of oceanic waters, conforming with hydrological data assessed quite independently (cf. Rayner in Gunther, 1935; Hart, 1953 and Fig. 95 below).

In contrast to *Planktionella* most of the Discineae observed on these two surveys were distributed mainly inshore or over the continental shelf. The distribution of *Stephanopyxis turris*, one of the most numerous of these, is shown in Figs. 85 and 86. It can be seen that though it was clearly an essential coastal form, both in autumn and spring, *Stephanopyxis* was absent from the middle of the *Chaetoceros* zone at both seasons. Further, it was distributed rather more to the northward in spring (Fig. 86)

than in autumn (Fig. 85). This feature cannot be explained by the seasonal shift in temperature alone, for the species is common in coastal waters round Cape Province, to the south of the area surveyed, at most seasons, and indeed all round the coasts of South Africa. A stenohaline tendency, such as that which seems to account for a similar distribution of the dinoflagellate *Dinophysis tripos*, might be partly responsible, since the region from which these species seem to be absent corresponds with the
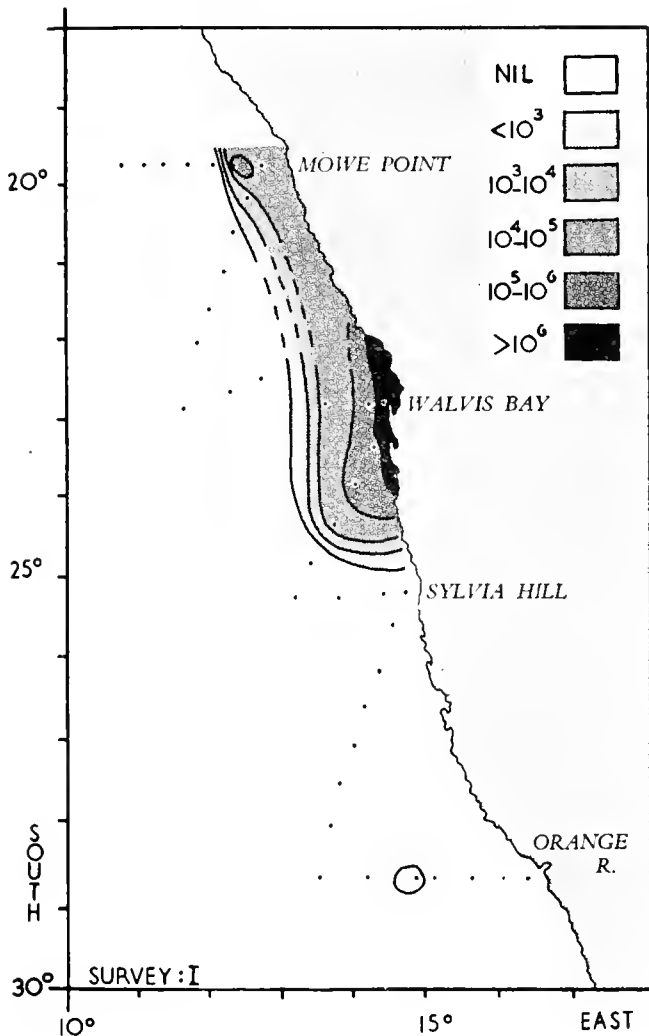
Fig. 85. Distribution of *Stephanopyxis turris*, survey I, March 1950. (Station numbers are shown in Fig. 1.)
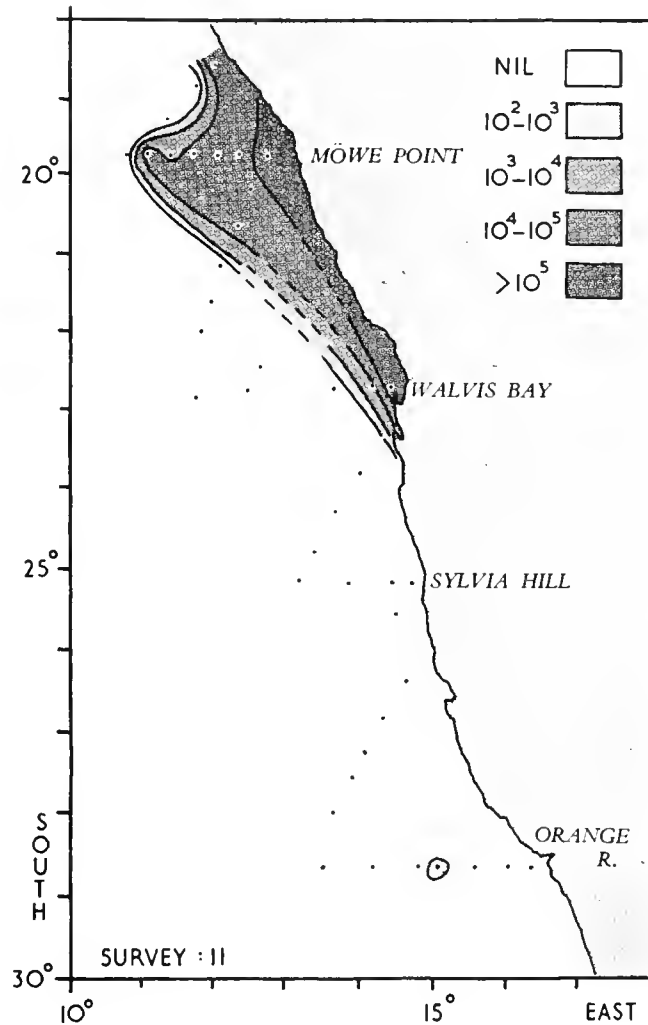
Fig. 86. Distribution of *Stephanopyxis turris*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

area of maximum negative salinity anomaly. The reduction in salinity is but slight, however, and *Stephanopyxis* shows so much adaptability elsewhere that an excluding effect of the superabundant chaetocerids, operating physically by crowding and/or chemically by noxious external metabolites (cf. Lucas, 1947) seems a more reasonable hypothesis.

Fig. 87 shows the distribution of *Eucampia zoodiacus* during the first (autumn) survey, when it seemed to be strictly confined to the rich coastal waters from Luderitz Bay northwards. The only Biddulphioid diatom observed in large quantities in any of these samples, the species was not seen at all in spring; when the group—almost exclusively a coastal one—was represented by forms such as *Eucampia cornuta*, *Biddulphia longicruris*, *B. regia* and *Cerataulina pelagica*, irregularly distributed and all in very small numbers. *Eucampia zoodiacus* seems to be a coastal form tending to flourish late in

the succession so far as this region is concerned, its autumn distribution being rather similar to that shown by *Stephanopyxis turris*, but without the apparent inhibition in the richest part of the *Chaetoceros* zone.

Asterionella japonica was the most abundant of the 'Pennatae' in the rich coastal waters, sometimes extending seawards, but in comparatively small numbers, as can be seen from Figs. 88 and 89. It was quite uninhibited by the huge quantities of chaetocerids, among which it flourished during the autumn
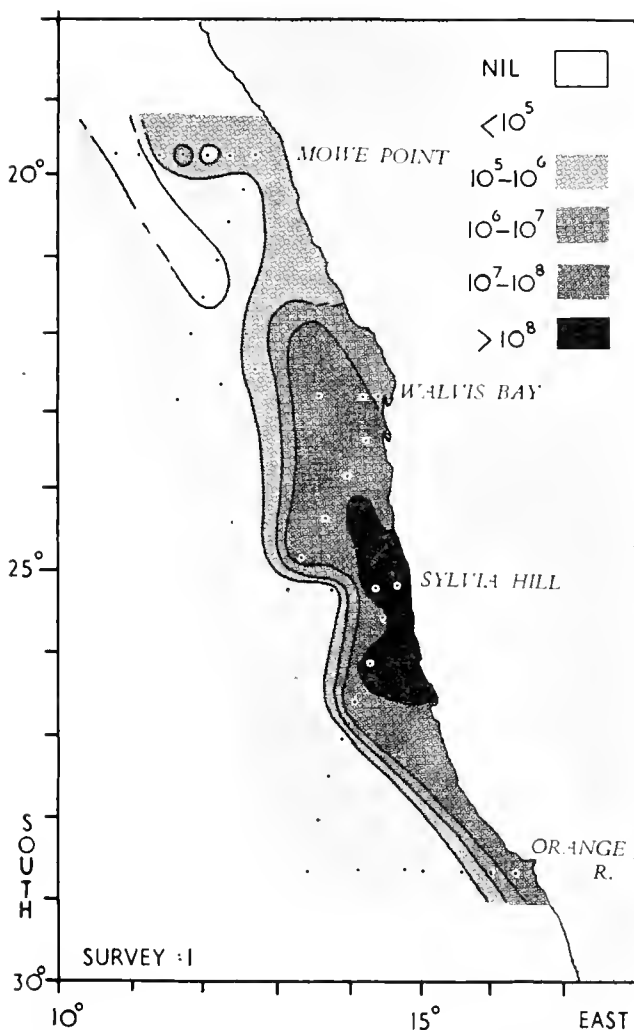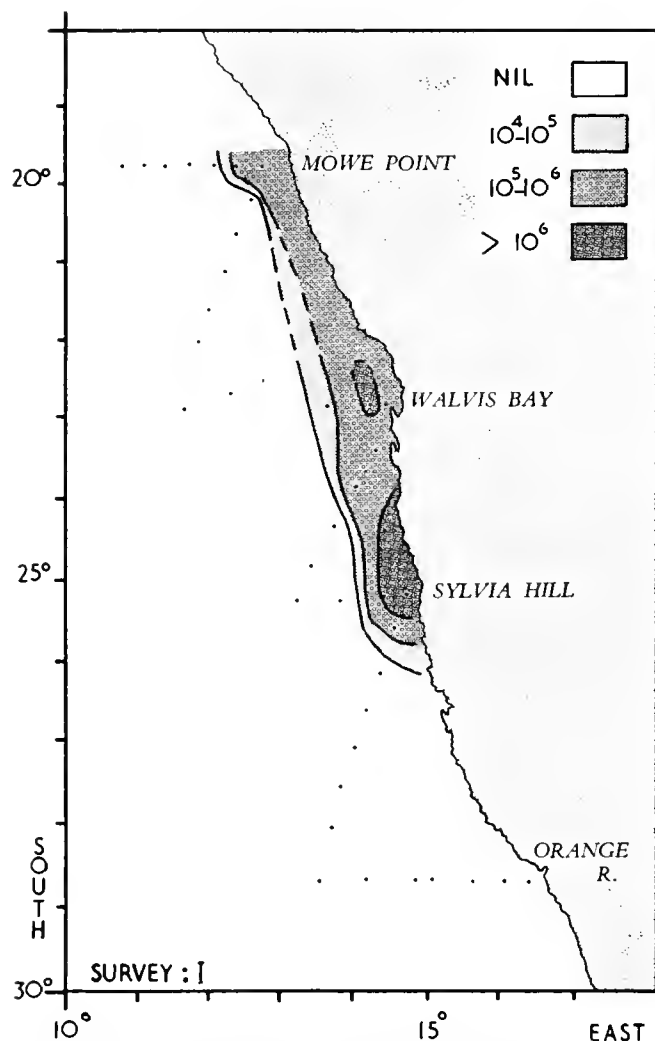

Fig. 87. Distribution of *Eucampia zoodiacus*, survey I, March 1950. (Station numbers are shown in Fig. 1.)
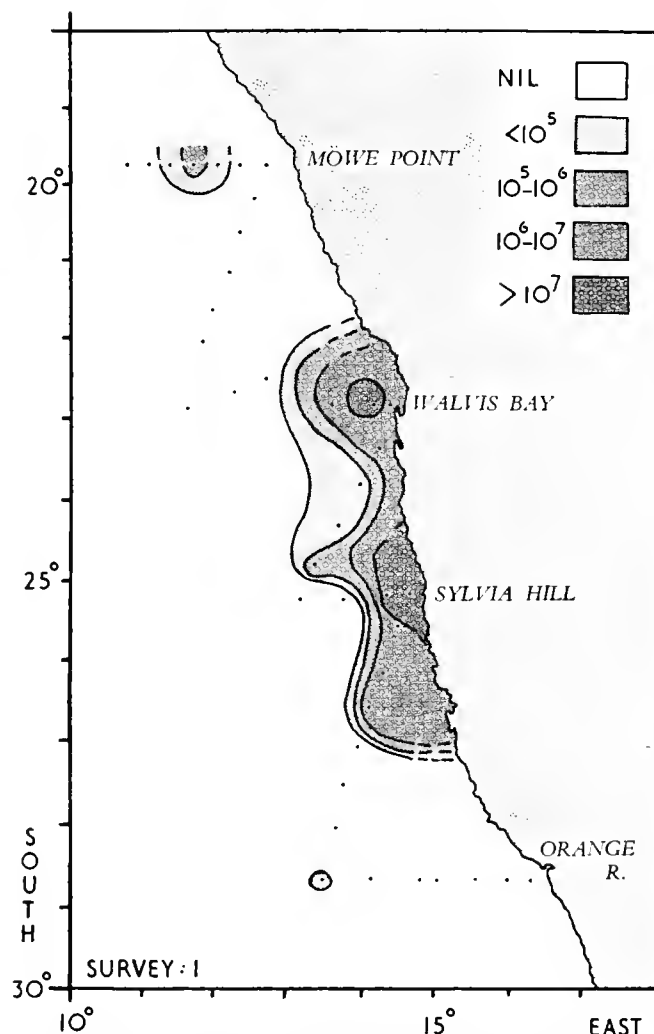
Fig. 88. Distribution of *Asterionella japonica*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

survey. Less numerous, but almost equally widespread in spring. The narrowing of the coastal zone and apparently increased tendency towards fanning-out of the coastal waters in the extreme north of the area at that season were features shown in some degree by other important inshore species.

The distribution of both the species of *Fragilaria* met with is shown in Figs. 90 and 91. *Fragilaria karsteni* proved to be the most strictly coastal of the diatoms encountered in the plankton here during both surveys; one might almost describe it as neritic. Though somewhat less widespread in autumn than it was during the spring survey, the heaviest individual hauls of the species were obtained in autumn near Walvis Bay.

Fragilaria granulata was a species of the outer shelf stations and offshore waters found mainly in

spring. It can be seen that its distribution never overlapped that of *F. karsteni* during these two surveys, and this emphasizes the extent to which the latter can be regarded as an 'indicator' of inshore conditions.

Two abundant 'Pennatae' have not been dealt with in this series: *Nitzschia delicatissima* and *N. seriata*. They tended to be irregularly distributed, perhaps reaching their greatest relative
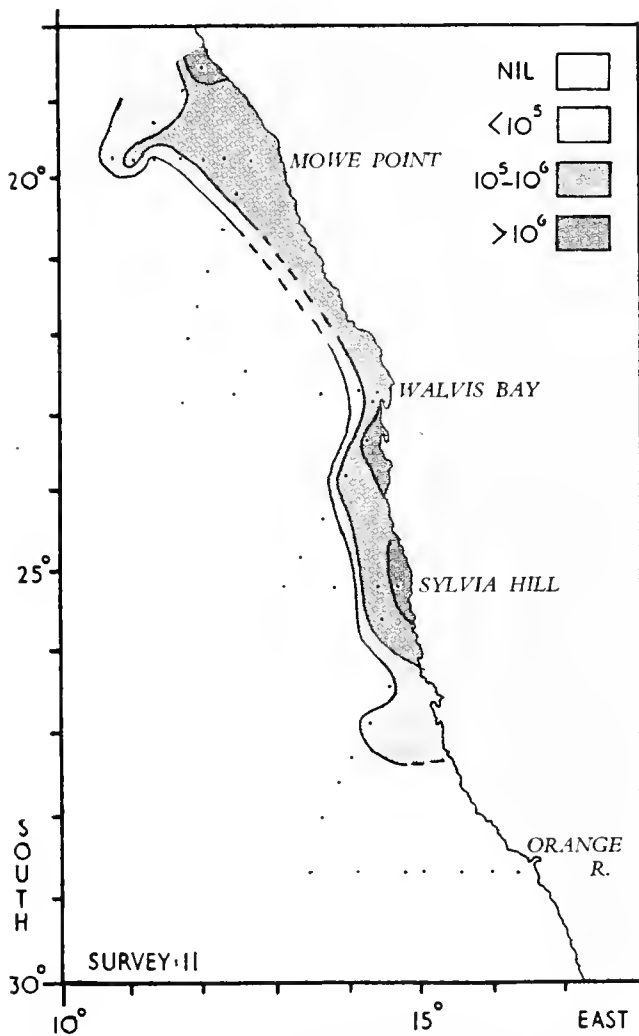
Fig. 89. Distribution of *Asterionella japonica*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)
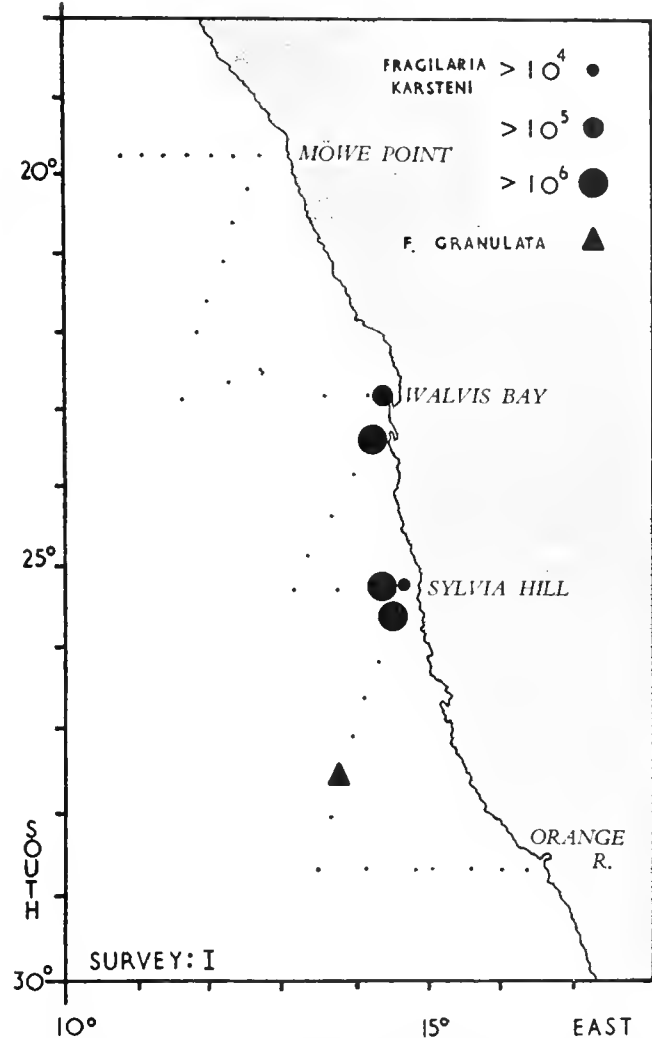
Fig. 90. Distribution of *Fragilaria karsteni* and *F. granulata*, survey I, March 1950. (Station numbers are shown in Fig. 1.)

importance in outer shelf-waters. Since they are among the most completely cosmopolitan of all marine plankton diatoms and, moreover, very difficult to separate with certainty when working at the speed necessary to obtain counts, it is scarcely surprising that they did not show such well-defined distributional trends as most other members of the group.

Figs. 92 and 93 show the relative importance (percentage of total diatoms) of *Thalassiothrix longissima*, the most essentially oceanic of the 'Pennatae' in this area, to be considerable at the offshore stations, where the total phytoplankton was poor. It was equally abundant at some rich shelf stations where, however, its proportion of the whole flora was insignificant.

This same method of treatment was also found necessary to show the high relative importance of the solenoid group offshore during the second survey only. Here they were definitely dominant, and the

offshore flora proved richer at that season than it had been during autumn. Though essentially holo-planktonic, the highly cosmopolitan species concerned easily attain greater numbers nearer land at other times and in other areas, although rarely achieving dominance there. Fig. 94 shows the solenoids as a percentage of total diatoms during the second (spring) survey only. The individual species mainly concerned showed a fairly definite sequence as the survey proceeded from south to north. To the south, far out off Luderitz Bay, *Rhizosolenia alata* was dominant. Proceeding northwards this was
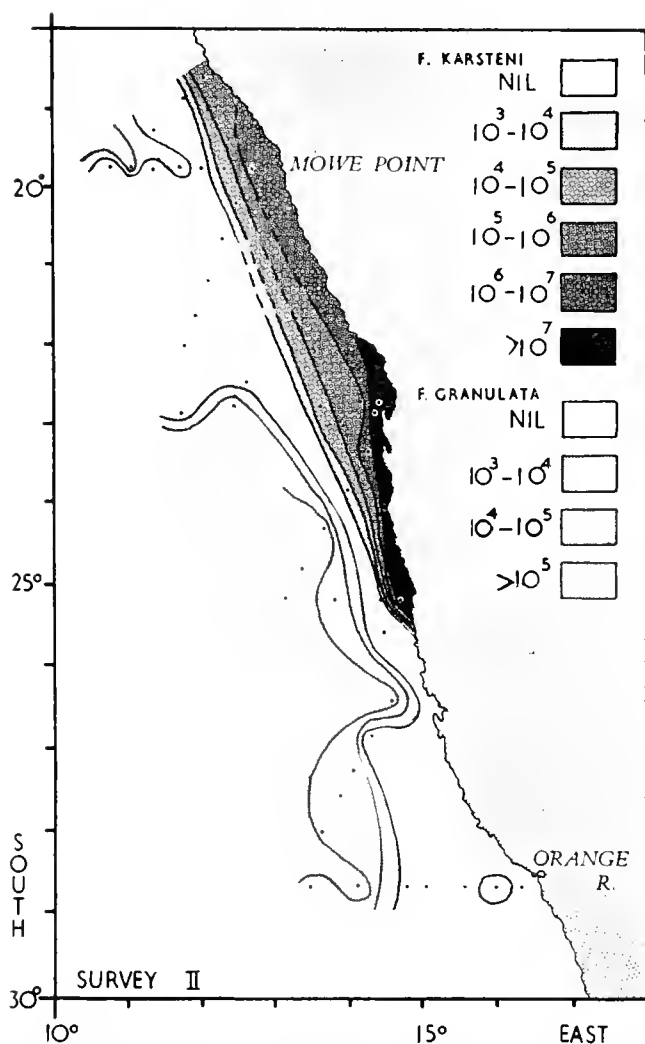
Fig. 91. Distribution of *Fragilaria karsteni* and *F. granulata*, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)
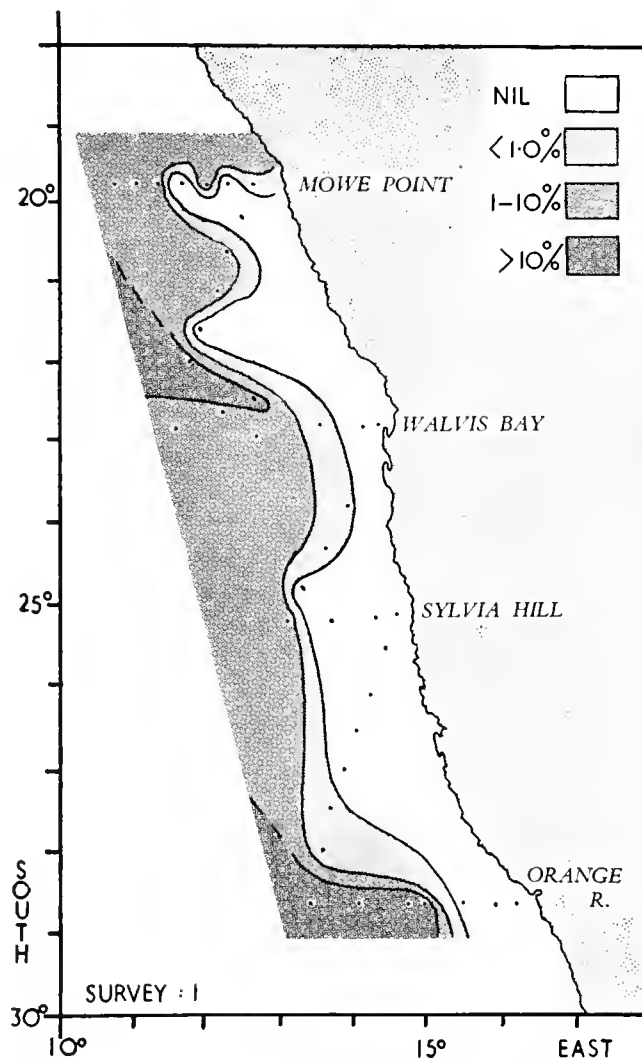
Fig. 92. Distribution of *Thalassiothrix longissima*, survey I, March 1950. Expressed as a percentage of the total diatoms. (Station numbers are shown in Fig. 1.)

succeeded by *R. styliformis*, more or less co-dominant with varying proportions of *R. alata*, these last being superseded in the extreme north of the area studied by *Dactyliosolen mediterraneus*.

In Fig. 95 an attempt has been made to demonstrate another aspect of distributional study, the development of a localized flora where the distinctive offshore and inshore populations most nearly approached each other, near the northern limits of the rich upwelling zone in autumn. The distributions shown are estimated numbers of *Planktoniella sol*, regarded as the characteristic offshore form; *Goniaulax spinifera*, the dinoflagellate predominating in the intervening 'patch';[1] and the estimated

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[1] The word 'patch' is here used in its generally accepted sense to describe the area where *Goniaulax* predominated. It is *not* intended to denote exceptional population density as in descriptions of visibly discoloured areas resulting from water-

group totals for the chaetocerids, with their pronounced maximum of development inshore. A degree of overlapping in the horizontal plane seems reasonably accounted for by vertical layering, for which there is some hydrological evidence. The point cannot be established from plankton data alone.

The presence of the *Goniaulax* patch just where the intrusive tongues of oceanic water extend farthest inshore seems strongly suggestive of mixing between the two types of surface-water. Some time-lag— general slowing of dispersive agencies—must also be postulated, to permit development of the third
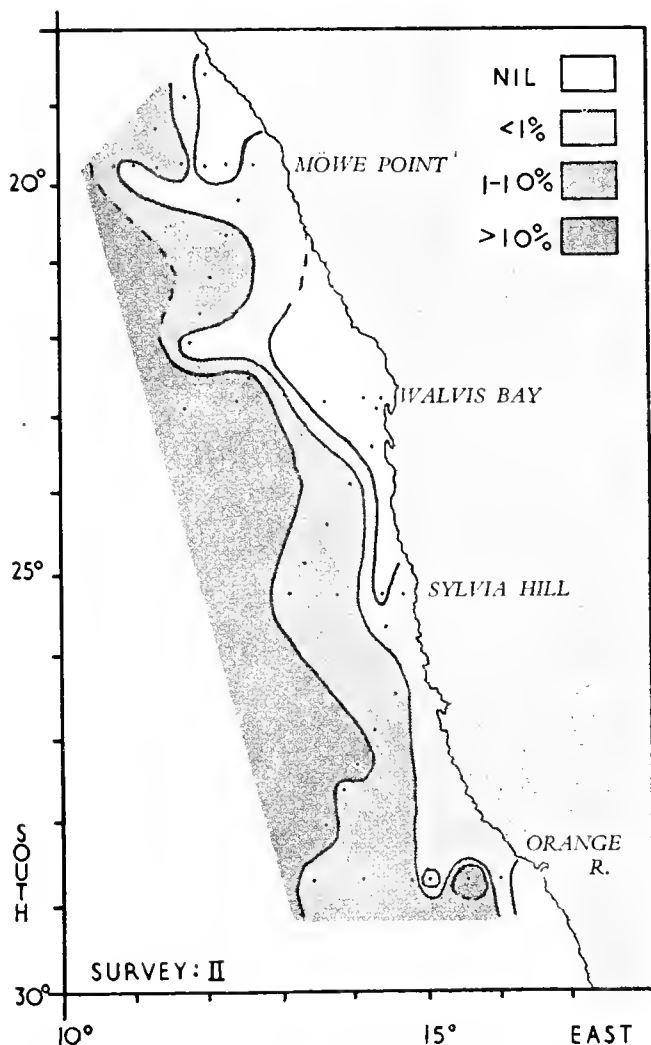
Fig. 93. Distribution of *Thalassiothrix longissima*, survey II, September–October 1950. Expressed as a percentage of total diatoms. (Station numbers are shown in Fig. 2.)
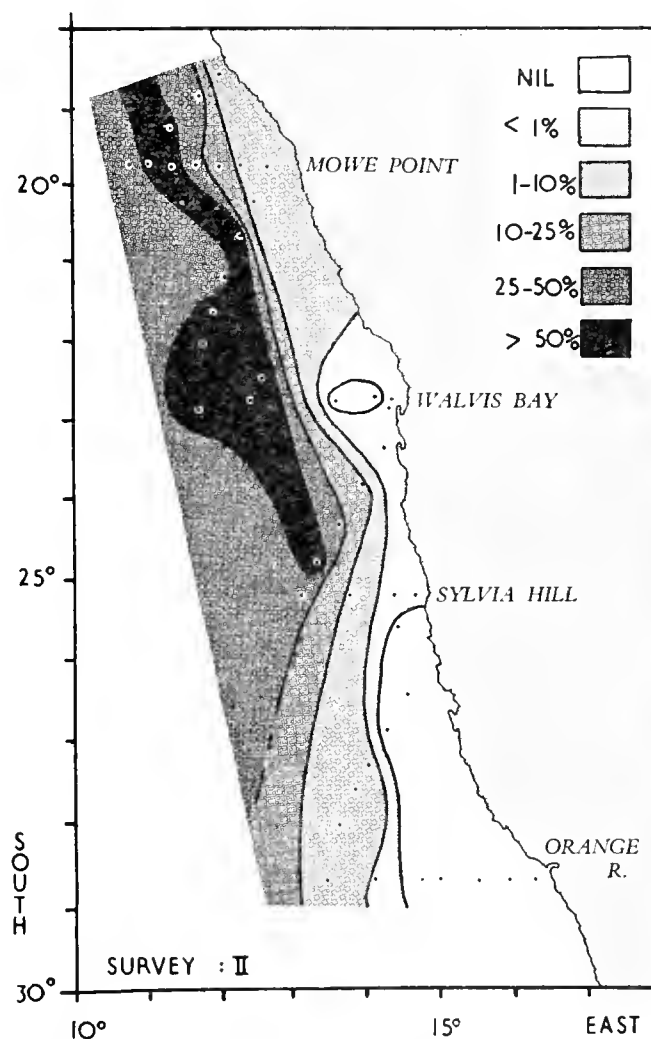
Fig. 94. Distribution of the Soleniineae expressed as a percentage of the total diatoms, survey II, September–October 1950. (Station numbers are shown in Fig. 2.)

distinctive localized type of flora. Much of our evidence points to the prevalence of the conditions required for this immediately prior to the autumn survey. The relatively high stability of the surface-layers, temperature and salinity distribution, and several features of the plant population combine to show that upwelling activity was then much reduced, and the plant succession at or just beyond its peak. Relatively 'old' surface-water from inshore, such as these conditions imply, should mix more readily with the offshore water than would that cooled by recent upwelling.

bloom formation. *Goniaulax* spp. have been known to cause water-bloom elsewhere, but such discoloured water as we were able to sample during these surveys was caused by other organisms. This does not preclude the probability that it may sometimes form blooms in this area—perhaps at other seasons.

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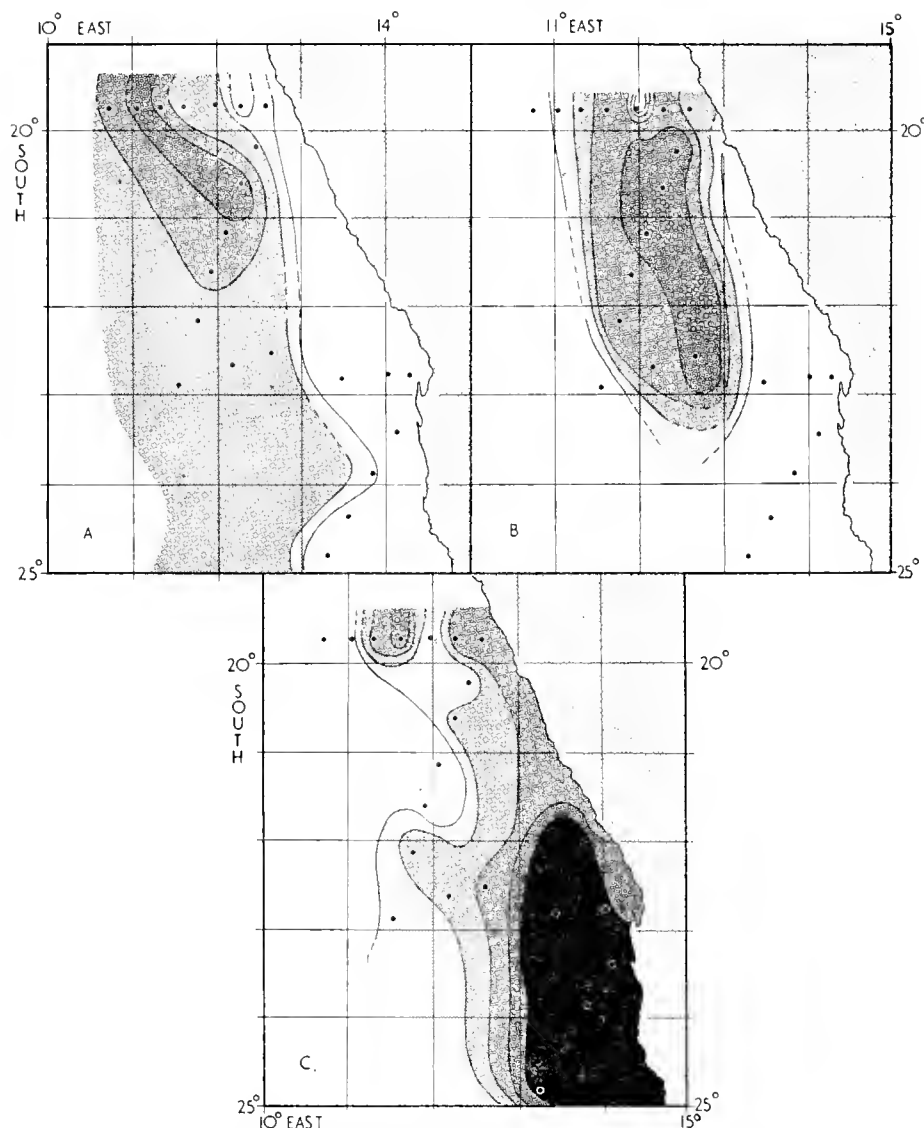
Fig. 95. Distribution of (A) *Planktoniella*, (B) *Goniaulax*, and (C) *Chaetoceros* between Möwe Point and Sylvia Hill, survey I, March 1950. Where there is no shading none was recorded. The lightest shading represents estimates of $< 10^4$ per net haul, the next 10^{4-5}, and so on.

OBSERVATIONS ON DISCOLOURED WATER

Large areas of the sea near Walvis Bay were discoloured 'blackish' by diatoms during our first survey, the general appearance being dark green to black, and opaque, very similar to that described in arctic regions by Brown (1868) and found by him to be due to diatoms also. In the Benguela current we found the inshore chaetocerids, especially *Chaetoceros didymum* and *Asterionella japonica*, to be the species chiefly responsible. Within this same region, however, were many more localized brownish or khaki-coloured discolorations, forming irregular bands and streaks roughly parallel with the coast, sometimes associated with foam streaks and lanes of dead and dying macroplankton—mainly ctenophores and salps—at the surface. A minor fish mortality had occurred near Walvis Bay just before we got there.

Three samples from some of these more strikingly discoloured waters were obtained off Sandwich Harbour (about 22° 30′ S. and 10 sea-miles offshore). Subsequent detailed microscopic examination of these yielded the results shown in Tables 18, 19 and 20.

Table 18. *Sample A of discoloured water near Sandwich Harbour. Collected at 13.45 hr. on 9 March 1950. Mixed, fractionized and diluted so that contents of 2·5 ml. could be counted direct, several counts being summed. Factor to reduce numbers to cells/ml. × 0·4*

Species or category	No. counted	×0·4≃esti-mated no. of cells/ml.	Estimated area in optical section μ²/ml.	Estimated volume μ³/ml.	% by number	% by area	% by volume
Peridinium triquetrum	387	155	44,795	217,000	40·38	20·53	13·9
Asterionella japonica	324	130	15,600	286,000	33·79	7·15	18·3
Prorocentrum micans	137	55	33,880	374,000	14·33	15·53	23·9
Thalassiosira spp.	52	21	28,000	292,000	5·44	12·83	18·7
Stephanopyxis turris	16	6	17,280	210,000	1·67	7·92	13·4
Peridinium spp.	16	6	74,400	150,000	1·67	34·09	9·6
Chaetoceros didymum	6	2	1,200	9,000	0·63	0·55	0·6
Eucampia zoodiacus	6	2	1,500	8,000	0·63	0·69	0·5
Nitzschia delicatissima	4	2	72	200	0·42	0·03	0·01
Chaetoceros curvisetum	3	1	300	2,200	0·31	0·14	0·1
Small 'Pennatae'	2	—	—	700	0·21	—	0·04
Staphylocystis sp.	2	3	1,200	1,200	0·21	0·55	0·1
Copepod egg	1	—	—	12,000	0·10	—	0·8
Small Dinophyceae non det.	2	—	—	500	0·21	—	0·03
Total Dinophyceae	544	218	153,475	742,700	56·80	70·42	47·53
Total diatoms	411	164	64,252	808,100	43·10	29·44	51·65
Other organisms	1	1	300	12,000	0·10	0·14	0·80
Total microplankton	956	383	218,227	1,562,800	—	—	—

The area in optical section of the total organisms in 1 ml. of this sample, when spread over a Sedgwick-Rafter counting-chamber, would thus be about 500 Whipple's International Standard Units, or 0·2 parts per thousand, and their volume some 1·5 parts per million of water. (The Sedgwick-Rafter cell, 5 × 2 cm. in area and with sides 1 mm. deep, holds 1 ml. of fluid spread over an area of 10 cm. (= 10⁹ μ²). One W.I.S.U. is a square 20 μ on one side (= 400 μ²). One ml. = (10¹² μ³).)

Table 19. *Sample B of discoloured water near Sandwich Harbour. First of two collected at 14.10 hr. on 9 March 1950. Noted as 'Khaki coloured water, reddish at a distance'. 1/8 of 10 ml. of the well-mixed sample, i.e. of 0·55 ml., examined direct by drop method and counts summed. Factor to express results as approx. nos. cells/ml. × 1·8*

Species or category	No. counted	×1·8≃esti-mated no. of cells/ml.	Estimated area in optical section μ²/ml.	Estimated volume μ³/ml.	% by number	% by areas	% by volume
Peridinium triquetrum	1,530	2,754	795,906	3,855,600	86·55	80·29	55·34
Asterionella japonica	122	220	26,400	484,000	6·91	2·66	6·95
Eucampia zoodiacus	25	45	33,750	180,000	1·41	3·40	2·58
Small 'Pennatae'	23	41	4,100	32,800	1·29	0·41	0·47
Thalassiosira spp.	22	40	56,000	568,000	1·26	5·65	8·15
Peridinium spp., small	20	36	18,000	813,600	1·13	1·82	11·68
Prorocentrum micans	10	18	11,088	115,200	0·57	1·12	1·65
Stephanopyxis turris	7	13	37,440	455,000	0·41	3·78	6·53
Chaetoceros constrictum	4	7	4,375	22,400	0·22	0·44	0·32
Tintinnidae	2	4	3,600	400,000	0·13	0·36	5·74
Nitzschia delicatissima	1	2	72	200	0·06	0·01	0·01
Cast skins of nauplii	1	2	600	40,000	0·06	0·06	0·57
Total Dinophyceae	1,560	2,808	824,994	4,784,400	88·25	83·23	68·67
Total diatoms	204	368	162,137	1,742,400	11·56	16·35	25·01
Other organisms	3	6	4,200	440,000	0·19	0·42	6·31
Total microplankton	1,767	3,182	991,331	6,966,800	—	—	—

Area in optical section of organisms in 1 ml. in Sedgwick-Rafter counting-chamber: about 2478 W.I.S.U., or nearly 1 part per thousand. Volume nearly 7 parts per million.

Table 20. *Sample C of discoloured water near Sandwich Harbour. Collected immediately after Sample B (Table 19), but in a streak of noticeably more turbid water 'Khaki–coffee coloured'. 0·25 ml. of well-mixed sample examined by drop method and counts summed. Factor to express results as approx. nos. cells/ml. × 4*

Species or category	No. counted	× 4 ≏ esti- mated no. of cells/ml.	Estimated area in optical section μ²/ml.	Estimated volume μ³/ml.	% by number	% by area	% by volume
Peridinium triquetrum	1,363	5,452	1,575,628	7,632,800	88·36	76·13	61·12
Asterionella japonica	74	306	36,720	673,200	4·96	1·77	5·39
Small 'Pennatae'	48	192	19,200	153,600	3·11	0·93	1·23
Peridinium spp.	10	40	258,000	904,000	0·65	12·47	7·24
Thalassiosira spp.	9	36	50,400	511,200	0·58	2·43	4·09
Chaetoceros constrictum	7	28	17,500	89,600	0·45	0·85	0·72
Stephanopyxis turris	6	24	69,120	840,000	0·39	3·34	6·73
Nitzschia delicatissima	6	24	864	2,400	0·39	0·04	0·02
Chaetoceros compressum	5	20	8,800	40,000	0·32	0·42	0·32
Prorocentrum micans	4	16	9,856	102,400	0·26	0·48	0·82
Chaetoceros dichaeta	3	12	4,800	108,000	0·19	0·23	0·86
Eucampia zoodiacus	2	8	6,000	32,000	0·13	0·29	0·26
Tintinnidae	2	8	7,200	800,000	0·13	0·35	6·40
Rhizosolenia setigera	1	4	5,600	600,000	0·06	0·27	4·80
Total Dinophyceae	1,377	5,508	1,843,484	8,639,200	89·27	89·08	69·18
Total diatoms	161	654	219,004	3,050,000	10·58	10·57	24·42
Other organisms	2	8	7,200	800,000	0·13	0·35	6·41
Total microplankton	1,540	6,170	2,069,688	12,489,200	—	—	—

Area in optical section of the organisms in 1 ml. in Sedgwick-Rafter counting-chamber: about 5160 W.I.S.U., or 2+ parts per thousand. Volume about 12·5 parts per million.

These tables allow comparisons, not only of the constituents, but also of the relative density of the microplankton in each sample in terms of numbers, area in optical section, and volumes, per millilitre. It is seen that sample *C* (Table 20) was by any standard nearly twice as dense as *B*. Sample *A* was much thinner, but the ratio varied little in terms of numbers, area or volume.

As to the constitution of the samples it appears that the small dinoflagellates *Peridinium triquetrum* and *Prorocentrum micans* were the main constituents of the thinnest of these samples (Table 18). with quite a high proportion of *Asterionella* and other inshore diatoms. The two richer samples (Tables 19 and 20) show a definite 'bloom' of *Peridinium triquetrum*, the other constituents providing less than 12% of the total number of organisms estimated.

Peridinium triquetrum, a neritic species of very wide distribution, has been recorded 'blooming' in association with a fish mortality on at least one previous occasion, at Rostock in the Baltic on 10 October 1917 (Lindemann, 1924, who called it by its old name *Heterocapsa triquetra*). Lindemann's plankton observations were only made after a considerable search for other possible causes of the catastrophe had proved fruitless. The *Peridinium triquetrum* was co-dominant with *Krypto-peridinium foliaceum* and other microplanktonic organisms were present only in quite insignificant proportions.

Our Benguela current findings, added to Lindemann's observations, might seem to suggest *Peridinium triquetrum* as a probable 'cause' of the Walvis Bay mortalities, but it has to be remembered that in both instances the mortality had begun before the observations on the bloom were made. The bloom may or may not have been present when the fish were killed. Braarud (1945) has shown that very high production of *P. triquetrum* (and sometimes of *Prorocentrum* also) may occur in heavily

polluted waters, inimical to most other marine plankton organisms, in the inner Oslo Fjord. Thus it even seems possible that these blooms might be the result, rather than the cause, of the mortalities.

The seemingly conflicting statements on the nature of the discolorations so often seen near Walvis Bay do seem to be partially resolved by our observations. Gilchrist's (1914) early insistence upon the vast proliferations of diatoms in the area are amply confirmed. Then to the dinoflagellate blooms described above we can add one of ciliate Protozoa (considerably to the northward but still within the Benguela current area) which was sampled at the end of the second survey. Further we have little doubt that Marchand's contention that blooms due to *Noctiluca miliaris* also occur there will eventually be vindicated.[1]

In the past each commentator has tended to assume that the most recently identified bloom-forming organism was responsible for all the other macroscopically similar visual effects reported from the area. This was natural enough when direct observations were few and often obscurely recorded. The point which we can claim from our results is that blooms—visible discolorations—due to widely differing types of organisms may occur (mostly at different times no doubt) within the same relatively small sea area.

The estimates of area and volume of the bloom-forming organisms in Tables 18–20 have been made from the means of numerous measurements and approximation to the nearest geometrical figure. They do not pretend to be precise, but are unlikely to show positive error. They are given here in the hope that the relative quantities of plant substance represented by counts of the various species may be better appreciated with their aid. The areas in particular may interest those familiar with Whipple's ([1889], 1908) concept of the International Standard Unit, a square $20\,\mu$ on the side viewing the organisms in optical section, which was found very useful in practical limnological work. These findings suggest that it could be very useful in marine work also, but it has to be borne in mind that it is only in the study of these blooms (or in cultures) that the marine plankton worker ever encounters populations approaching the densities shown in Tables 18–20. Usually he has to deal with populations sparser by at least one order of magnitude than these. It is in fresh waters that such concentrations are frequently met with.

From the volumes the relative size relations of the more important plants found in these samples can be computed, with the results shown in Table 21. This shows, for example, that here one cell of the diatom *Stephanopyxis turris* was roughly eleven times as big as one cell of *Chaetoceros constrictum*, and twenty-five times as big as one of the dominant dinoflagellates, *Peridinium triquetrum*. Obviously it is important to establish dominance by methods going further than the counts alone when possible. Lohmann (1908) made an attempt in this direction by analogous methods in Kiel Bay, but generally speaking the range of size variation, even within single species of phytoplankton organisms, is so great that application of the method to large series would demand recalculation of volume factors every few samples, and the increase in time and labour involved would make it quite impracticable.

An intense red discoloration observed close inshore (WS 1107) in 13° 05′ S. at the conclusion of the second survey proved to be due to swarming of a ciliate protozoan *Cyclotrichium meunieri* Powers (probably synonymous with *Halteria rubra* Lohmann = *Mesodinium rubrum* Lohmann (Apstein).) Large-scale discolorations caused by this organism had previously been seen in the waters round Cape Peninsula (Hart, 1934).[2] When swarming this animal distorts itself or bursts spontaneously in

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[1] *Trichodesmium thiebautii*, the Cyanophycean that so often forms blooms in many parts of the tropical and subtropical Atlantic, probably does so in the Benguela current area on occasions. It was dominant in some of our poorer plankton hauls, but we have not yet seen it there in bloom-forming quantities.

[2] An unfortunately premature communication, missing Lohmann (1908), Apstein (1908), Paulsen (1909) and even Darwin (1839). I tried to rectify these mistakes in a second letter published in 1943, but cannot blame myself for having missed Powers (1932). Our ship left Europe in 1933 when his work had barely had time to reach European libraries, and being

any quantity of water small enough to permit one to examine it microscopically, the process being accentuated in greater or less degree by addition of all the narcotics or fixatives tried hitherto. Bary and Stuckey (1953) found very dilute hydrogen peroxide the best narcotic, leaving a larger minority of relatively little distorted specimens available for subsequent fixation. When the ciliates burst many of the coloured 'platelets' (Lohmann)[1] are extruded. The enormous numbers of these in the sample from WS 1107 were observed in the field by Clarke and Currie, and their likeness to Hematococcidae noted. The preserved sample, however, showed the characteristically shrunken remains of many of the ciliates that had not burst (cf. Lohmann, 1908, fig. 7, no. 53, p. 201), so many indeed, that the discoloured water must have contained not less than 13,370 per ml. It seemed pointless to attempt counting of the freed 'platelets' since the vast majority had unquestionably been aggregated (in varying numbers) within ciliates before the sample was taken. A small *Gymnodinium* sp., one other small dinoflagellate and a *Coscinodiscus* sp. were present in very small numbers (up to 7 per ml.).

Table 21. *Size inter-relations of organisms from the samples taken off Sandwich Harbour, 9 March 1950. Selected to cover the dominants and species covering the extremes of variation in volume; others omitted*

	Rhizo-solenia setigera	Stephano-pyxis turris	Thalas-siosira spp.	Chaeto-ceros dichaeta	Proro-centrum micans	Chaeto-ceros con-strictum	Peri-dinium trique-trum	Approx. volume (estimated) in μ^3 ($1\,\mu^3 = 10^{-12}\,ml.$)
Rhizosolenia setigera	1	4	10½	16½	23	47	107	150,000
Stephanopyxis turris	4	1	2½	4	6	11	25	35,000
Thalassiosira spp.	10½	2½	1	1½	2	4½	10	14,200
Chaetoceros dichaeta	16½	4	1½	1	1½	3	6	9,000
Prorocentrum micans	23	6	2	1½	1	2	4½	6,400
Chaetoceros constrictum	47	11	4½	3	2	1	2	3,200
Peridinium triquetrum	107	25	10	6	4½	2	1	1,400

Dense swarms of this ciliate have thus been seen near the two ends of the region where the Benguela current is best defined. It seems unlikely from what is known of its proclivities elsewhere, that the conditions of negative anomaly of temperature and salinity in between would prove exclusive to it. Probably, therefore, before long some more fortunate observer will be able to add it to the list of diverse forms now known to give rise to visual discolorations there at various times.

THE DISTINCTION BETWEEN OFFSHORE AND INSHORE DIATOM FLORAS

Yet another array of the data, based upon arbitrarily selected distance limits, serves to show up the distinctive features of the flora of the inshore and offshore waters during the two surveys, providing a basis for ecological characterization of the species within each of the main diatom groups. Some repetition of points made in discussing distribution at group level is involved here, but seems to the writer (T.J.H.) to be unavoidable if the apparent anomalies due to the cosmopolitan and panthalassic species are to be made clear.

The arbitrary limits first chosen were: stations within 40 miles from the coast regarded as within an inshore region, and stations more than 100 miles from the coast, regarded as definitely oceanic or

without fore-knowledge that we were to encounter his ciliate more than a year later, we could hardly be expected to have included it in the small working library carried at sea! I have hoped to clear up some of the misunderstandings following my 1934 letter in a separate publication, but the topic seems dangerous! (T.J.H.).

[1] These were described as 'most probably symbiotic algae', and given the name *Erythromonas haltericola* by Lohmann (1908). Concerning them also Apstein (1908) wrote 'this is perhaps the alga living symbiotically in *Mesodinium rubrum*'. I mentioned them as 'Coloured granules some 4μ in diameter, possibly symbiotic zoochlorellae' in ignorance of the earlier work, though this may now seem to be incredible (T.J.H.).

offshore. It then became clear that the results from the wide intermediate or 'outer shelf' zone (40–100 miles from the land), besides yielding the obvious intermediate averages, also showed up the extent to which surface-waters of the two more distinctive types were overstepping the arbitrary limits chosen on each of the two surveys. The full value of this feature could only be realized by considering individual species on each line of stations as we have already treated the main groups. Though this is impracticable here it still seemed worthwhile to include average values for the arbitrary 'outer shelf' zone, despite the masking effect of the 'averaging' process in the following tables, for the reason given above.

For this special purpose the anomalous results from the Orange river line were not considered, and this leaves thirty-two stations at repeat positions on each of the two surveys for comparison.

Table 22 shows the average estimated diatom totals per net haul, and the average totals and percentages for each main group as previously defined, when the data are arrayed in this fashion. It also provides in effect a crude summary of the line-upon-line treatment of main group-distribution already given. It is essential that the relative quantities indicated should be kept in mind if the percentages for species within each group, given in Tables 13–17, are to be properly understood.

Table 22. *Average estimated diatom totals, with average numbers and percentages of the main diatom groups, when the data are grouped according to distance from the coast as shown. (Results from the Orange river line excluded)*

	Average estimate of total diatoms per net haul	Average Discineae		Average Biddulphiineae		Average Chaetoceraceae		Average Soleniineae		Average 'Pennatae'	
		Numbers	%	Numbers	%	Numbers	%	Numbers	%	Numbers	%
Inshore stations < 40 sea miles from the coast											
First survey (autumn)	85,157,491	2,836,753	3·33	1,528,631	1·80	68,024,177	79·88	877,582	1·03	11,890,348	13·96
Second survey (spring)	65,979,818	884,173	1·34	72,400	0·11	58,486,700	88·64	146,455	0·22	6,390,090	9·68
'Outer shelf' stations 40–100 sea miles from the coast											
First survey (autumn)	15,712,563	217,934	1·39	14,672	0·09	14,673,800	93·39	80,419	0·51	725,738	4·62
Second survey (spring)	2,158,972	82,025	3·80	225	0·01	811,229	37·57	727,091	33·68	538,402	24·94
Offshore stations > 100 sea miles from the coast											
First survey (autumn)	156,287	20,972	13·42	None seen	—	22,480	14·38	31,510	20·16	81,323	52·03
Second survey (spring)	779,740	17,880	2·29	None seen	—	139,260	17·86	515,400	66·10	107,200	13·75

From Table 22 it appears that:

(1) the **Discineae** were of minor importance offshore during the first (autumn) survey. Elsewhere they formed but a small proportion of the total diatoms, their greater numbers inshore notwithstanding during both surveys.

(2) The **Biddulphiaceae** were of very minor importance inshore, mainly in autumn. Very small quantities of this group were observed on the 'outer shelf', and none at the offshore stations.

(3) The **Chaetoceraceae** were strongly dominant inshore at both seasons, rather more so in spring than in autumn. They were also strongly dominant on the 'outer shelf' in autumn, but much less so during spring. Offshore they were outnumbered by other groups at both seasons.

(4) The **Soleniineae** were the dominant group offshore during spring. They ranked second to

the chaetocerids on the 'outer shelf' in spring, and to the 'Pennatae' offshore in autumn. Inshore they were relatively unimportant at both seasons.

(5) The 'Pennatae', though generally much less abundant than the chaetocerids, ranked second to that group at the inshore stations during both surveys. They were rather more important in autumn than in spring right inshore, but this trend was reversed on the 'outer shelf'. Offshore the group was relatively much more important in autumn than during spring, although slightly more abundant in the richer spring catches.

Table 23. *Relative importance of the group Discineae, and percentage of the several species, within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore <40 sea-miles from land		'Outer shelf' 40–100 sea-miles from land		Offshore >100 sea-miles from land	
	First survey (autumn)	Second survey (spring)	First survey	Second survey	First survey	Second survey
(a) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(b) Average total Discineae	2,836,753	884,173	217,934	82,025	20,972	17,880
b/a as percentage	3·33	1·34	1·38	3·80	13·44	2·29
Average total for each category as percentage of the average total for the group (M category/b as %)						
Skeletonema costatum	– –	1·56	1·15	—	—	—
Stephanopyxis turris	16·0	6·46	2·52	12·12	—	—
Thalassiosira condensata	2·8	—	0·92	—	—	—
T. excentrica	19·5	—	11·41	—	45·0	—
T. hyalinum	6·9	—	0·16	—	—	—
T. rotula	13·8	—	—	—	—	—
T. subtilis	27·2	50·43	70·63	11·82	—	6·0
Thalassiosira spp. non det.	13·3	34·73	2·75	23·20	—	30·2
Bacterosira fragilis	0·03	—	—	—	—	—
Coscinodiscus gigas	—	—	—	—	0·3	—
C. janischii	<0·01	—	—	—	—	—
Coscinodiscus spp. non det	0·34	5·61	0·20	14·85	—	9·8
Actinocyclus spp. non det.	0·01	—	—	—	—	—
Planktoniella sol	0·02	0·11	9·84	32·15	54·7	47·3
Hemidiscus cuneiformis	—	0·03	0·01	0·46	—	—
Actinoptychus senarius	<0·01	0·15	0·01	0·64	—	6·7
Asterolampra spp. non det.	—	0·41	—	—	—	—
Asteromphalus heptactis	0·08	0·49	0·40	4·76	—	—

Table 23, which shows the relative importance of the various Discineae when the data are grouped in this fashion, provides strong evidence of the neritic or inshore habit of most of the species. Though several extended to the outer shelf, eleven out of the eighteen categories were not seen farther offshore. *Planktoniella sol* was clearly the most essentially oceanic species. Although sufficiently adaptable to occur inshore its numbers increased very markedly with increasing distance from land during both surveys. The remainder of the scanty offshore representation of the group consisted chiefly of more panthalassic, but equally cosmopolitan, species like *Thalassiosira excentrica* and *T. subtilis*.

The most important Discineae inshore were *Stephanopyxis turris* and various species of *Thalassiosira*. They were most prominent in autumn (or late in the succession) while the less numerous forms provided greater *relative* proportions of the group totals in the smaller spring catches (e.g. *Asteromphalus heptactis*).

The Biddulphiaceae (Table 24) were very sparsely represented in the area surveyed. Inshore, in autumn, *Eucampia zoodiacus* was of some slight importance, and just extended on to the outer shelf area. There, however, *Cerataulina pelagica* formed a slightly higher proportion of the very small group average. *Eucampia zoodiacus* was not observed during the spring survey, when *Biddulphia longicruris* provided the bulk group totals. Biddulphiaceae were not observed more than 100 miles offshore during either survey, though one of the species recorded, *Hemiaulus hauckii*, has been seen far out in the South Atlantic on other occasions, and should probably be regarded as an oceanic form.

Table 24. *Relative importance of the group Biddulphiaceae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore <40 sea-miles from land		'Outer shelf' 40–100 sea-miles from land		Offshore >100 sea-miles from land	
	First survey (autumn)	Second survey (spring)	First survey	Second survey	First survey	Second survey
(a) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(b) Average total Biddulphiaceae	1,528,631	72,400	14,672	225	—	—
b/a as percentage	1·80	0·11	0·09	0·01	—	—
Average for each category as % of (b)						
Biddulphia longicruris	—	99·05	—	—	—	—
Cerataulina pelagica	1·66	0·95	53·04	—	—	—
Triceratium favus	0·02	—	—	—	—	—
Hemiaulus hauckii	—	—	1·38	—	—	—
Eucampia cornuta	—	—	—	100	—	—
E. zoodiacus	98·32	—	45·58	—	—	—

The tremendous local importance of the Chaetoceraceae is clear from Table 25, which also illustrates the very cosmopolitan nature of the species of this family. All of those which we were able to identify are widely known from other regions, ranging from 'boreal' to 'warm temperate', with some which extend into truly tropical surface-waters as well.

Within this area most of them were essentially neritic—inshore and outer shelf species—and of these a majority were more abundant in autumn, or late in the succession, than in spring. Most important of all, however, were three panthalassic species which must be among the most widespread and abundant of all marine plankton diatoms: *Chaetoceros compressum*, *C. constrictum* and *C. curvisetum*. The first two of these were almost equally abundant at both seasons, while *C. curvisetum*, the most numerous of all the diatoms according to these estimates, showed a distinct maximum in spring, though vast numbers had been found in the autumn samples also.

Of the more strictly neritic species *C. didymum* was the most abundant, especially in autumn, when vast numbers of the very characteristic resting spores were present. *C. subsecundum* and most of the other neritic species of lesser but still considerable local importance, for example, *C. affine*, *C. costatum*, *C. debile*, *C. teres*, *C. tetras*, showed a similar time distribution. *C. strictum*, however, showed a strong inshore maximum during the spring survey.

The most abundant and widespread of the oceanic species, *C. convolutum*, showed a spring maximum here. So also did two oceanic forms of lesser importance in these samples: *C. atlanticum* and *C. peruvianum*.

The 'ecological characterization' of the species of this most important and difficult genus of marine plankton diatoms arrived at by the late Professor Gran, through continued efforts towards improving his system of 'plankton elements' as applied in the northern hemisphere (Gran in Murray and Hjort, 1912; Gran and Braarud, 1935), can thus far be extended to this southern area without serious

discrepancy. Two well-known cosmopolitan species, however, were found to be distributed here rather differently from what might have been expected from their previously known dispositions elsewhere. *C. lorenzianum*, usually regarded as a neritic form, here reached its greatest relative importance in the offshore samples, with a strong spring maximum. Conversely *C. decipiens*, one of the most widespread of all oceanic species, was more plentiful here inshore in spring than it had been offshore during the autumn survey.

Table 25. *Relative importance of the group Chaetoceraceae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore < 40 sea-miles from land		'Outer shelf' 40–100 sea-miles from land		Offshore > 100 sea-miles from land	
	First survey (autumn)	Second survey (spring)	First survey	Second survey	First survey	Second survey
(a) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(b) Average total Chaetoceracea	68,024,177	58,486,700	14,673,800	811,229	22,480	139,260
b/a as percentage	79·87	88·64	93·41	37·58	14·40	17·86
Average for each category as percentage of the average total for the group (*M* category/*b* as %)						
Chaetoceros affine	0·12	1·67	1·32	1·00	—	- -
C. atlanticum	—	< 0·01	—	3·09	—	3·66
C. compressum	14·18	18·70	42·92	37·91	26·69	17·23
C. constrictum	21·76	11·65	13·59	22·06	—	23·48
C. convolutum	0·01	< 0·01	0·33	3·93	10·68	11·25
C. costatum	0·79	—	1·10	0·19	—	—
C. curvatum	—	—	0·01	—	—	- -
C. curvisetum	22·12	45·67	3·57	6·92	56·94	21·97
C. debile	4·60	0·41	0·45	—	—	—
C. decipiens	0·36	5·05	0·08	5·21	4·89	—
C. didymum	5·93	1·89	1·96	0·98	—	1·29
C. didymum (resting spores)	13·57	0·02	6·99	—	- -	- -
C. difficile	1·63	1·35	5·48	1·48	—	1·48
C. holsaticum	—	0·34	—	—	—	—
C. imbricatum	—	—	0·25	—	—	—
C. laciniosum	< 0·01	0·02	—	—	—	—
C. lorenzianum	0·31	0·85	—	5·17	—	17·92
C. peruvianum	0·05	—	0·05	0·29	—	0·60
C. pseudocrinitum	0·13	—	6·05	—	—	- ·
C. sociale	—	0·39	0·37	—	—	2·58
C. strictum	1·84	10·93	3·98	2·09	—	- -
C. subsecundum	6·28	0·30	1·20	9·68	- -	- -
C. subsecundum (resting spores)	0·22	—	- -	—	- -	—
C. teres	1·04	< 0·01	3·98	—	—	—
C. tetras	0·11	0·66	2·37	—	- -	—
C. van heurckii	4·95	0·10	1·39	—	0·80	—
Chaetoceros spp. non det.	—	—	2·57	—	—	—

This evidence of a more panthalassic trend than was hitherto suspected for these two species, in a region of exceptionally steep temperature gradients and rapid changes in conditions of the milieu, is not surprising. Indeed, the general conformity of the majority of the genus to the distributional pattern that might have been predicted from their known proclivities elsewhere, seems even more remarkable to me under these conditions, which seem quite sufficient to account for the occurence of both warm-water and cold-water forms together within a limited area. When the need for a reasonable

amount of elasticity in the application of the ecological terms is borne in mind, the value of the earlier work seems to me most amply justified (T.J.H.).

Within the group Soleniineae, consisting almost wholly of holoplanktonic cosmopolitan forms, the difficulty involved in any attempt at further ecological characterization is augmented by the almost completely panthalassic nature of some of the most important species. This results in some species showing maximum importance offshore under oceanic conditions in spring, but inshore under neritic conditions in autumn or vice versa. The compromise implicit in the word panthalassic seems as far as one can go in any attempt at brief summary of their distributional tendencies!

Table 26. *Relative importance of the group Soleniineae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore <40 sea-miles from land		'Outer shelf' 40–100 sea-miles from land		Offshore >100 sea-miles from land	
	First survey (autumn)	Second survey (spring)	First survey	Second survey	First survey	Second survey
(a) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(b) Average total Soleniineae	877,582	146,455	80,419	727,091	31,510	515,400
b/a as percentage	1·03	0·22	0·51	33·68	20·16	66·10
Average for each category as percentage of the average total for the group (M category/b as %)						
Bacteriastrum hyalinum	0·21	—	1·17	—	—	—
B. varians	0·16	—	—	0·02	—	—
Rhizosolenia alata	1·83	0·41	36·78	21·11	36·92	8·67
R. cylindrus	—	—	—	0·02	—	—
R. fragillissima	—	—	0·58	—	—	—
R. hebetata	9·34	0·76	49·94	5·40	49·62	4·85
R. imbricata	1·08	0·19	1·63	2·11	3·81	2·25
R. robusta	0·05	—	0·06	—	—	—
R. setigera	—	66·29	—	3·09	—	0·12
R. simplex	—	—	5·80	0·67	9·65	—
R. stolterfothii	0·74	—	—	—	—	—
R. styliformis	0·13	0·60	0·45	30·25	—	74·69
Guinardia sp. non det.	—	—	0·09	—	—	—
Leptocylindrus danicus	15·88	4·66	2·72	—	—	—
Dactyliosolen mediterraneus	70·53	2·23	—	36·90	—	9·19
Corethron criophilum	0·05	24·86	0·77	0·43	—	0·23

A few species, notably *Leptocylindrus danicus* with its maximum late in the succession, were definitely limited to the neritic samples in both series. *Rhizosolenia setigera*, seen only during the spring survey, was important inshore at that season.

The most completely cosmopolitan species, that helped to render this group dominant offshore in spring and of considerable importance there in autumn also, should probably be regarded as essentially oceanic, but so adaptable that they may attain higher numbers among the vastly heavier catches of other forms in enriched coastal waters on some occasions. A similar difficulty is found when one attempts ecological classification of some of the dominant phytoplankton species of antarctic surface waters (Hart, 1942).

In the Benguela current area the important panthalassic solenoids were: *Rhizosolenia alata* and *R. hebetata*, especially late in the succession inshore, but also augmenting the group's spring maximum offshore; *R. styliformis*, here showing a more distinct oceanic trend and spring maximum; and

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Dactyliosolen mediterraneus. This last provides the greatest enigma, being found in great numbers inshore during the first (autumn) survey, but also among the dominants on the outer shelf and offshore (especially in the northern part of our area) in spring. It is possible that more restricted temperature requirements may account for this anomaly if the spring temperatures inshore are suboptimal for this species. Conversely, *Corethron criophilum*, undoubtedly an oceanic form in most of its phases, here showed a very definite maximum inshore in spring, which might be explained by 'preference' for lower temperatures.

The ecological relationships of the 'Pennatae' (Table 27) at group level are not very clear, chiefly because it is an arbitrary 'unnatural' assemblage of the diverse 'reversionary plankton forms' with sundry tychopelagic species, introduced solely to assist in concentrating the data to within manageable proportions. At the specific level, however, most of them can be seen to conform to definite distributional trends much more clearly than most of the solenoids.

Fragilaria karsteni, Asterionella japonica and the rarer tychopelagic species all had a definitely inshore, neritic distribution. *Fragilaria karsteni* was most abundant in spring and *Asterionella japonica* in autumn. *Thalassiothrix longissima* was an offshore form with a spring maximum, and so in the main was *Fragilaria granulata*, which never overlapped its congener.

The only important 'Pennatae' not clearly assignable to one of the distributional trends that we now feel to be recognizable (somewhat dimly, perhaps) are *Nitzschia delicatissima* and *N. seriata*. These are among the most ubiquitous, cosmopolitan, panthalassic diatoms known, as all marine plankton workers must agree. Here they were prominent at all distances from land especially in spring. *N. seriata* was the more important inshore, while *N. delicatissima* showed maximum relative importance in the scanty offshore catches in autumn, though not nearly so numerous there as it was on the 'outer shelf' during both surveys.

Table 27. *Relative importance of the group Pennatae, and percentage of the several species within the group. Results arrayed according to distance from the land as shown, omitting those from the Orange river line*

	Inshore < 40 sea-miles from land		'Outer shelf' 40–100 sea-miles from land		Offshore > 100 sea-miles from land	
	First survey (autumn)	Second survey (spring)	First survey	Second survey	First survey	Second survey
(a) Average total diatoms	85,157,491	65,979,818	15,712,563	2,158,972	156,287	779,740
(b) Average total 'Pennatae'	11,890,348	6,390,090	725,738	538,402	81,323	107,200
b/a as percentage	13·96	9·68	4·62	24·94	52·03	13·75
Average for each category as percentage of the average total for the group (*M* category/*b* as %)						
Fragilaria granulata	—	0·18	0·06	9·95	—	6·04
F. karsteni	12·77	48·95	—	0·21	—	—
Asterionella japonica	64·15	5·42	62·78	6·01	—	3·36
Thalassiothrix longissima	0·06	1·54	6·12	18·60	31·24	29·04
Thalassionema nitzschioides	—	4·35	0·01	1·95	—	1·68
Striatella sp. non det.	—	—	—	0·08	—	—
Navicula membranacea	—	0·03	—	—	—	—
Navicula spp. non det.	0·04	0·17	1·18	0·06	—	—
Pleurosigma capense	0·01	0·01	—	—	—	—
Pleurosigma sp. non det.	0·02	—	—	—	—	—
Nitzschia closterium	0·81	—	2·37	0·23	11·80	0·78
N. delicatissima	0·31	8·24	17·96	16·96	55·04	19·36
N. longissima	0·06	—	—	0·52	—	—
N. seriata	21·77	31·11	9·40	45·43	1·92	39·73

The cosmopolitan distribution of marine plankton diatoms and the 'ecological' characterization' of the more important species from the Benguela current

A further selection of the most important or typical diatom species observed within the area permits concise illustration of the extremely cosmopolitan distribution of these in other regions, so that it is the relative importance of the various forms rather than their mere presence and absence that must be studied before relationships between the floras and their 'conditions of existence' begin to be perceptible. This further selection has been used to give examples of the brief 'ecological characterizations' of species, on Gran's lines, that are so helpful in the attempt to perceive some order in the ever-changing phytoplankton communities.

Table 28 shows reported occurrences of these typical Benguela current species in various other regions, ranging from the North Atlantic to the antarctic zone of the southern ocean. Some of these have received much less complete coverage than others, and yet other regions might be added, especially around Japan (cf. Aikawa, 1936), but the table is surely adequate to show the very cosmopolitan distribution of most of the species. This fact was generally recognized by most of the earlier phytoplankton workers (cf. Gran and Braarud, 1935, and Aikawa 1936, among others), but it probably became so obvious to them that they rarely sought to stress it. The species listed in Table 28 are selected on the ground that we have observed them to be dominant, typical or otherwise important in the Benguela current, and without reference to their occurrence elsewhere. But there is no reason to suppose that the less important or typical species—except perhaps the neritic ones (see below)—are any more restricted in their distribution. At least it can be said that of all the eighty-two species identified from the Benguela area so far, none are 'new to science'.

The supreme importance of the inshore chaetocerids (of the group Hyalochaete) in the upwelling regions, can only be fully appreciated when quantitative data are considered, but is still apparent here in the relatively large number of species recorded. It can also be seen that the holoplanktonic, mainly oceanic solenoids are perhaps the most completely cosmopolitan of all plankton diatoms, though panthalassic 'reversionary plankton forms' such as *Nitzschia seriata* are almost equally widely distributed.

The few important species that seem to be limited to the Benguela current area and adjacent South African coasts are all inshore ones: *Chaetoceros strictum* and *C. tetras*, *Fragilaria granulata* and *F. karsteni*. Certain other coastal species are recorded from comparatively few of the other regions mentioned, but since these include major upwelling regions their very widespread distribution is in no doubt. Further sampling will almost certainly reveal their presence in the less favourable intervening areas eventually, though probably in such small numbers as to form but an insignificant proportion of the sparse populations to be found there. These forms include *C. costatum*, recorded elsewhere from the coast of southern Europe and North Africa, California and Japan; *C. pseudocrinitum*, S. temperate coasts of Europe and California, and *C. van heurckii*, recorded only from California and the Madras coast of India among the other localities considered. *Nitzschia longissima* also has a comparatively restricted occurrence, so far as it is yet known, being recorded only from the other African localities, California and Japan.

Proceeding to brief 'ecological characterizations' of the several species on the basis of our observations in the Benguela current area, it is necessary to make the proviso that maximal occurrence during spring or autumn may indicate *either* a normal seasonal effect *or* merely that these species tend to flourish earlier or later in a succession that quite probably repeats itself several times in the course of a year, as the more or less persistent upwelling system waxes and wanes.

Table 28. *Distribution in other regions, defined below (with sources).* × *positive records*

Selected abundant or typical Benguela current species	South African waters			North and Tropical Atlantic				Indian Ocean	West Pacific		East Pacific		Southern Ocean	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
DISCINEAE														
Stephanopyxis turris	×	×	×	×	—	×	×	×	—	—	×	×	×	×
Thalassiosira subtilis	×	—	×	×	—	×	×	×	×	×	×	×	×	×
Planktoniella sol	×	×	×	×	—	×	×	×	×	×	×	×	×	×
BIDDULPHIACEAE														
Biddulphia longicruris	×	—	—	—	—	—	×	×	—	—	×	×	—	—
Eucampia zoodiacus	×	—	×	×	×	×	—	×	—	×	×	×	—	—
CHAETOCERACEAE														
Chaetoceros affine	—	×	×	×	×	×	×	×	×	×	×	×	—	×
C. atlanticum+var. *neapolitanum*	× ×	—	× ×	× ×	×—	× ×	——	——	× ×	× ×	× ×	——	×—	×—
C. compressum	—	—	×	×	×	×	—	×	×	×	×	—	×	—
C. constrictum	×	×	×	×	×	×	—	—	—	—	×	—	—	—
C. convolutum	×	—	—	×	×	×	—	—	—	—	×	—	×	×
C. costatum	—	×	—	×	—	×	—	—	—	×	×	—	—	—
C. curvisetum	×	—	—	×	—	×	—	×	—	×	×	×	—	—
C. debile	—	×	—	×	×	×	—	—	×	×	×	—	×	—
C. decipiens	—	—	×	×	×	×	×	—	—	×	×	×	×	×
C. didymum	×	×	×	×	×	×	×	×	—	×	×	×	×	×
C. difficile	×	×	—	×	—	—	—	×	—	×	×	—	×	—
C. laciniosum	—	—	—	×	×	×	—	×	—	×	×	—	—	×
C. lorenzianum	×	×	—	×	—	×	×	×	×	×	×	×	×	×
C. peruvianum	×	×	×	—	—	×	×	×	—	×	×	×	×	×
C. pseudocrinitum	—	—	×	×	×	—	—	—	—	—	×	—	—	—
C. sociale	×	×	—	×	×	—	×	×	—	×	×	×	×	×
C. strictum	×	×	—	—	—	—	—	—	—	—	—	—	—	—
C. subsecundum	×	—	—	×	×	×	—	—	—	—	×	—	—	×
C. teres	×	—	—	×	×	×	—	—	—	×	×	—	—	—
C. tetras	×	×	—	—	—	—	—	—	—	—	—	—	—	—
C. van heurckii	×	—	—	—	—	—	—	×	—	—	×	—	—	—
SOLENIINEAE														
Rhizolenia alata	×	×	×	×	×	×	×	×	×	×	×	×	×	×
R. hebetata	×	×	—	×	×	×	×	×	×	×	×	×	×	×
R. imbricata	×	×	×	×	×	×	×	×	—	×	×	×	×	×
R. setigera	—	—	—	×	×	×	×	×	×	×	×	—	—	—
R. styliformis	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Leptocylindrus danicus	×	—	×	×	×	×	—	×	×	×	×	×	—	—
Dactyliosolen mediterraneus	—	—	×	×	×	×	—	—	—	×	×	—	—	—
Corethron criophilum	×	×	×	×	×	×	×	×	×	×	×	×	×	×
PENNATAE														
Fragilaria granulata	×	—	×	—	—	—	—	—	—	—	—	—	—	—
F. karsteni	×	×	—	—	—	—	—	—	—	—	—	—	—	—
Asterionella japonica	×	—	×	×	×	×	×	×	×	×	×	—	×	—
Thalassionema nitzschioides	×	×	×	×	×	×	×	×	—	×	×	×	×	×
Thalassiothrix longissima	×	—	×	×	×	×	×	×	×	×	×	×	×	×
Nitzschia closterium	×	×	—	×	×	×	×	×	—	×	×	—	×	×
N. delicatissima	×	—	—	×	×	×	—	—	—	×	×	—	×	×
N. longissima	×	—	—	—	—	×	×	—	—	×	—	—	—	—
N. seriata	×	×	×	×	×	×	×	×	×	×	×	×	×	×

1 Atlantic coast of Cape Province (Boden, 1950).
2 Between Cape Town and Port Elizabeth (Karsten, 1906).
3 Agulhas current (Hendey, 1937).
4 'Northern Seas' (Lebour, 1930).
5 Bay of Fundy, Gran and Braarud, 1935.
6 Temperate and subtropical North Atlantic, including Canary current (K. R. Gaarder, 1951).
7 Tropical Atlantic (Karsten, 1906, and others).
8 Madras coast of India (Subrahmanyan, 1946).
9 Chu San I. China, *ca.* 30° N. lat. (Sproston, 1949).
10 Pacific coast of Japan (Aikawa, 1936; Marumo, 1954; Takano, 1954).
11 Pacific coast of North America, including California current (Cupp, 1943; Sleggs, 1927; Allen, 1938).
12 Peru current (Hendey, 1937).
13 Subantarctic, mainly Atlantic sector (Hart, 1934; Hendey, 1937).
14 Antarctic (Hart, 1934, 1942; Hendey, 1937).

Stephanophyxis turris was here an inshore ('coastal' or 'neritic') species found mainly in the northern (warmer) part of the area surveyed. Much more abundant in autumn than during spring.

Thalassiosira subtilis had a panthalassic distribution. Maximal abundance inshore in autumn; greatest relative importance offshore during the spring survey.

Planktoniella sol. An oceanic species relatively important at sparsely populated offshore stations only, during both surveys.

Biddulphia longicruris. An inshore species frequent and 'typical' though never abundant, in spring samples; not yet observed at all in autumn ones at the dilutions necessary to obtain counts.

Eucampia zoodiacus. An inshore species with precisely the converse of the seasonal distribution of *Biddulphia longicruris.* *Eucampia zoodiacus* was not seen at all during analysis of the spring samples. In autumn it was abundant, sometimes one of the dominant species close inshore.

Chaetoceros atlanticum (type) mainly offshore with pronounced spring maximum.

Chaetoceros atlanticum var. *neapolitanum* even more definitely restricted to offshore waters than the type (with relatively high temperature) but also in some of the same samples.

Chaetoceros affine (syn. *C. Ralfsii*) here a strongly neritic species much more abundant in autumn than during spring.

Chaetoceros compressum was one of the most abundant species at both seasons inshore, but sufficiently panthalassic for the 'overspill' to dominate at a few of the sparser offshore catches as well.

Chaetoceros constrictum. Very important during both surveys. Distributed much like *C. compressum.*

Chaetoceros convolutum was mainly an offshore species most abundant during spring.

Chaetoceros costatum, an inshore species most numerous in autumn (or late in the succession).

Chaetoceros curvisetum, mainly inshore and with a spring maximum, but very important at both seasons. The most abundant species in these samples. Showed sufficient panthalassic tendency to dominate some offshore samples as well, like *C. compressum* and *C. constrictum,* which often occurred with it.

Chaetoceros debile. Inshore, most in autumn, very local here.

Chaetoceros decipiens. Panthalassic, though mainly offshore here, more in spring than in autumn.

Chaetoceros didymum. An inshore species with pronounced autumnal maximum, when the resting spores were even more abundant than the vegetative phase.

Chaetoceros difficile. Mainly inshore with autumn maximum.

Chaetoceros laciniosum. An inshore species, local here, with strong spring maximum.

Chaetoceros lorenzianum. Panthalassic here with spring maximum far offshore at the outer end of the Orange river line.

Chaetoceros peruvianum. Offshore form more abundant during spring than in autumn.

Chaetoceros pseudocrinitum. An inshore or shelf species here, most in autumn.

Chaetoceros sociale. A panthalassic species on its showing here, abundant at some very localized inshore stations, but relatively more important offshore in spring.

Chaetoceros strictum. An inshore species observed most abundantly during the spring survey.

Chaetoceros subsecundum. An inshore species with autumn maximum, when many of the characteristic resting spores were present.

Chaetoceros teres. An inshore species most abundant in autumn here.

Chaetoceros tetras. A very local species abundant at a few inshore stations, most in spring.

Chaetoceros van heurckii. An inshore species most abundant in autumn.

Rhizosolenia alata. Panthalassic rather than exclusively oceanic here, most important offshore in spring, but numerous during both surveys.

Rhizosolenia hebetata. Present here almost exclusively in the form (or phase) *semispina.* Was most numerous inshore in spring, but of much greater relative importance offshore, especially in autumn. Panthalassic seems a fairer description than oceanic for this extremely cosmopolitan form.

Rhizosolenia imbricata. Here var. *Shrubsolei* was more frequent than the type, but both were present in the same samples at times. Panthalassic, reaching its greatest relative importance offshore at both seasons.

Rhizosolenia setigera. An inshore form with spring maximum.

Rhizosolenia styliformis. Panthalassic, but mainly offshore with a pronounced spring maximum.

Leptocylindrus danicus. An inshore species most abundant in autumn.

Dactyliosolen mediterraneus. Panthalassic, maximum inshore in autumn, but offshore during the spring survey!? Stenothermal.

Corethron criophilum. Panthalassic here, where most were seen inshore or on the outer shelf in spring. Of its generally oceanic character in most phases there can be no doubt.

Fragilaria granulata. Panthalassic? Recorded here only from the outer shelf or even offshore, never overlapping with the next species. Not recorded elsewhere except off South Africa.

Fragilaria Karsteni. Very definitely neritic and with a spring maximum, but also quite abundant during the autumn survey. Recorded elsewhere only off Cape Province (Karsten (syn. *F. capensis*) Boden).

Asterionella japonica. An important inshore and outer-shelf species, especially in autumn when it was one of the few other species to rival the dominant chaetocerids in abundance, and partly responsible for visible discoloration of the water at some stations close inshore.

Thalassiothrix longissima, though never very abundant, was relatively important offshore at both seasons, rather more so in spring than during the autumn survey.

Thalassionema nitzschioides. An inshore species, very local in this area, chiefly in spring (or early in the succession).

Nitzschia closterium. Tychopelagic, a littoral species fairly frequent in plankton close inshore, but never abundant here.

Nitzschia delicatissima. Panthalassic, mainly offshore with an autumn maximum here.

Nitzschia longissima. Never abundant, but very characteristic of the inshore plankton here, especially on the spring survey. Possibly littoral, tychopelagic.

Nitzschia seriata. Panthalassic, abundant and important at both seasons studied. Most important offshore in spring, but more abundant inshore.

Comparing these ecological notes with those of other workers, principally Gran, Lebour, Braarud and Gran, Cupp and K. R. Gaarder, as referred to in the sources of Table 28, it appears that a large majority of the species considered important or typical in the Benguela area were disposed therein just as one would expect from their recorded distributions elsewhere. Minor modifications of previous ecological characterizations based on these results, and on earlier work in the southern ocean (Hart 1934, 1942), are suggested as follows:

Thalassiosira subtilis should probably be regarded as panthalassic rather than oceanic. Though cosmopolitan in the open oceans, it frequently attains greater abundance near land. Gaarder's (1951) note that though widespread in the Michael Sars material from the North Atlantic, the species was observed most abundantly close in to the Azores, accords with this view.

Conversely several of the dominant chaetocerids of the rich inshore waters, though undoubtedly neritic in the main as recorded elsewhere, showed a more or less pronounced panthalassic trend; since lesser numbers of them flourished sufficiently far offshore to dominate the sparser communities encountered there. This trend was most marked in *Chaetoceros Lorenzianum,* but was also shown by the three most abundant of all the diatoms met with: *C. compressum, C. constrictum* and *C. curvisetum.*

The inshore or neritic species *C. subsecundum* exhibited a striking seasonal difference from its known disposition in the northern hemisphere, where most observers have recorded a strong maximum in spring or early summer. On our two surveys it was relatively much more abundant in autumn. Possibly we missed an earlier maximum through lack of full seasonal coverage, which would show up any repetition of the succession at a shorter interval of time. Equally we may here have a real difference due to the 'conditions of existence', biological as well as physical. In the northern hemisphere the species has been regarded as arctic-boreal or boreal, but both Gaarder's results and our own show that it can flourish in much warmer temperate waters than the earlier records suggest, where it must find itself among a very different and much more varied phytoplankton community.

The holoplanktonic cosmopolitan solenoids: *Rhizosolenia alata* and *R. hebetata. f. semispina* would seem definitely better described as panthalassic rather than oceanic. Their dominance at certain sparsely populated oceanic stations is unquestioned, but at the same time they were often found in greater numbers among the rich *Chaetoceros* plankton close inshore. The same applies in a less marked degree to *R. imbricata* (mainly the variety *Shrubsolei*; the larger type phase was rarer and 'more

'oceanic' here, though they occasionally occurred in the same samples). Temperature is probably the factor involved, having regard to the distributional records of the two forms elsewhere (cf. p. 217).

Similarly *Corethron criophilum* and even the well-known *Rhizosolenia styliformis* both tended to display a more panthalassic trend than their usual designation as oceanic forms would lead one to expect. In support we may cite the abundant occurrence of *Corethron* (in some of its phases) close in to the land as well as offshore in the antarctic zone of the southern ocean, and the occurrence of almost pure communities of *Rhizosolenia styliformis* in the shallow waters of the North Sea (Hardy, 1923; Wimpenny, 1936).

Concerning *Dactyliosolen mediterraneus* previous opinions were 'neritic' (Lebour) and 'neritic, sporadically oceanic'. K. R. Gaarder (1951) found moderate numbers of it in samples from all over the area covered by the 'Michael Sars' to the west and south of the British Isles. In the Benguela material the species was locally abundant offshore in spring and inshore in autumn, suggesting that it thrives only within narrow limits of temperature (stenothermal, with optimum range about $15°$ to $19°$ C.). Certainly 'panthalassic' would seem to be the best brief description of its general distributional trend.

Finally, two of the most abundant 'pennatae', *Nitzschia delicatissima* and *N. seriata*, previous ecological descriptions of which range from 'perhaps oceanic, but often abundant inshore', to definitely 'neritic', would in the opinion of the writer (T.J.H.) be better described as panthalassic—expressing the duality of the best of the earlier descriptions in one word. They were numerous in both inshore and offshore samples in the area studied here, and also in antarctic seas (Hart, 1934, 1942).

These minor differences from previous brief ecological descriptions of the species are so few that it is the general concordance with the opinions of those with the greatest experience of working through large collections of material that is striking, encouraging the belief that in this direction at least plankton workers grope towards 'the truth' to some purpose. Although Gran's 'system of plankton elements' must necessarily be modified as data from the less-known sea-areas becomes available, the ideas implicit therein remain one of our greatest aids in the attempt to understand the relations between phytoplankton communities and their 'conditions of existence'.

This comparison of the diatom-flora of the Benguela current with those of other regions brings out one important point, implicit in much that has been published already, but little emphasized by the earlier authors: that there is a fundamental difference between the diatoms and, for example, the species of oceanic zooplankton, in the nature of their distribution.

Although there are some cosmopolitan species of zooplankton, the range of the majority is subject to some limit beyond which they are unknown. Where there is a region offering an environment similar to that occupied by such a species, but isolated from it, we normally find there a similar species, but a distinct one. Most of the plankton diatom species, however, excepting certain neritic, polar, or markedly stenothermal warm-water forms, are not limited in their dispersal by 'barriers' to anything like the same extent as the zooplankton. Many of the more cosmopolitan diatoms may turn up almost anywhere in the oceans of the world, and become locally important or even dominant, wherever the 'conditions of existence' best suit them.

It is for this reason that the plankton floras of adjacent water masses must be studied with more regard to the differing proportions of the various species within them, than to the presence or absence of particular forms.

ZOOPLANKTON

On both of the 'William Scoresby's' surveys net hauls were made to sample the zooplankton. Full particulars are given in the Station List (1953). On survey I these consisted of a series of vertical hauls with the 'Discovery' N 70 V net, and were taken only on the three main latitudinal lines of stations. On survey II the hauls were extended to include a surface haul with a metre stramin net (N 100 H) at all stations and in addition an oblique haul with a metre stramin and 70 cm. net (N 100 B, N 70 B) was made at all 'full stations'—that is, again on the latitudinal lines of stations.

One of us (T.J.H.) has sorted the zooplankton hauls from survey I, and the material has so far as possible been distributed to specialists in the various groups. Reports on some groups have already been published, and we present a synopsis of the findings of these. Where it has not yet been possible to find specialists to work up the groups, they have been provisionally identified and the results are used in the following general account, sometimes merely to give a picture of the distribution of the group as a whole. Some important groups, notably the Copepoda, have not yet been dealt with.

The zooplankton samples from survey II have not yet been sorted, apart from some groups—fish eggs and larvae, Cumacea and Chaetognatha—whose distribution had proved unusually interesting during the first survey. These results are included in the following account.

POLYCHAETA

Most of the polychaets in the collection were larval or juvenile forms. These have not yet been examined in detail and it is hoped that they will be dealt with separately at a later date. It is interesting to note, however, that some seemed to show a tendency towards a prolonged post-larval sojourn in the plankton over the regions where the bottom waters were exceptionally deficient in oxygen.

CHAETOGNATHA

The chaetognaths in the collection from survey I have been examined and identified by Mr P. M. David, and will be dealt with in a separate report by him. The following notes have been made from the figures kindly supplied by Mr David.

The distribution of the species seems to follow a rather similar pattern on all three lines of stations. Close to the coast in the surface-layers *Sagitta friderici* Ritter-Zahony was dominant. Immediately seawards of this, *S. serratodentata* Krohn became the dominant species, still, however, in the shallower waters of the continental shelf, although this latter species was also found in smaller numbers at the oceanic stations WS 977 and 996. *S. decipiens* (Fowler) occupied a position just off the edge of the continental shelf and generally somewhat deeper in the water column, the main centre of abundance varying from line to line in depths of about 100–400 m.

Eukrohnia hamata (Mobius) was concentrated mainly farther seawards than the *Sagitta decipiens*, in the deeper layers, while above the *Eukrohnia hamata* population, varying numbers of *Sagitta minima* (Conant) and *S. lyra* (Krohn) were taken. Some numbers of *S. lyra* were also taken at station WS 978.

ENTOMOSTRACA

Dr J. P. Harding has very kindly confirmed the identification of the specimens of Cladocera which were picked out from the samples. Both *Evadne nordmani* Lovén and *Podon polyphemoides* Leuck. were present in the collections, and *Evadne nordmani* was the relatively more abundant species.

The Cladocera were present only at the stations lying close to the coast. Off Walvis Bay at WS 981, they reached their greatest concentration, more than 600 *Podon polyphemoides* and nearly 2200 *Evadne*

nordmani being present in the 50–0 m. haul. At the next station seawards, WS 980, they were only present in the 50–0 m. haul (one *Podon polyphemoides* and twenty *Evadne nordmani*), the 100–50 m. haul and all other hauls on this line of stations being devoid of Cladocera.

On the Sylvia Hill line only two *E. nordmani* were taken at the station closest to the coast (WS 989), and although no specimens were taken on the Orange river line, one specimen of *E. nordmani* was recorded farther south at WS 1043 on the second survey.

It was very noticeable during sorting how completely the Ostracoda gave way to Cladocera close in to the land on each line of stations. Here it seems that the marine ostracods constitute an essentially oceanic mid-water group, while the Cladocera were confined to the most neritic part of the coastal current. The two groups showed an almost complete absence of overlap in the first survey samples.

OSTRACODA

Mr E. J. Iles (1953) has published a report on the ostracods in the collection. Nearly all of these occurred at the offshore stations. As with the mysids, variety rather than numerical abundance characterized the group. Three genera were present, and of one of these, *Conchoecia*, twenty-three species occurred in the samples.

Four or five species of *Conchoecia* predominated, but by far the greatest number were contributed by the species *Conchoecia elegans* Sars.

C. elegans mainly inhabited the 500–250 m. layer off the edge of the continental shelf on the three main lines of stations, but there are also indications that it shows a vertical migration, similar to that described by Fowler (1909) in the Bay of Biscay, and more than eighty adults were found in the 50–0 m. layer at the night station WS 977.

C. nasotuberculata Müller, and *C. curta* Lubbock, both appeared to occupy a depth distribution similar to that of *C. elegans*, or perhaps at rather shallower levels. *C. alata* Müller was found at greater depths, 500 m. or more, while *C. symmetrica* Müller was amongst the deepest species of all, possibly even exceeding 1000 m., the greatest depth of the net hauls.

C. teretivalvata Iles occurred in quite large numbers in the shallower layers, i.e. in samples from 250–100 m., except at one station, WS 976, where an anomalous haul of twenty-four specimens occurred in the 750–500 m. layer.

As previously noted the ostracods did not overlap the Cladocera, and indeed at the inshore stations their niche appears to be filled by the latter group.

MYSIDACEA

Dr Tattersall (1955) has examined and reported on the collections of mysids,[1] and the following remarks are abstracted from her report.

Only at one station, WS 1002, were large numbers of individuals taken. Here, in the 50–0 m. haul, there were over 450 specimens of the gregarious mysid, *Gastrosaccus sanctus* (van Beneden). One small juvenile specimen of the same species was taken rather farther seaward at station WS 1000. Both these stations are somewhat farther south than is normally recorded for this species.

In spite of the paucity of numbers in the net hauls at the other stations, there was a richness of species in which ten genera and sixteen species were recorded. Many of these occur within the known geographical range of the species. *Boreomysis rostrata* Illig occurred in the deeper 750–500 m. hauls at the offshore stations. Two species, however, show an interesting deviation from their normal range. *Dactylamblyops hodgsoni* Holt and Tattersall has previously been recorded only from deep waters in

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[1] Her report is on a much larger collection which includes those from the Benguela current.

the Southern Ocean, and at station WS 976 one juvenile specimen was taken in the 1000–750 m. haul. The other species, *Euchaetomera zurstrasseni* (Illig), although originally recorded from the Indian Ocean west of the Chagos Islands, has only been recorded once in the waters to the west of Cape Town, and is usually only taken in the far south of the Atlantic Ocean. One specimen occurred at station WS 976.

CUMACEA

The Cumacea were identified by Dr N. S. Jones and the following account has been abstracted from his report on the group (1955).

Four genera and five species were present in the samples, but only the genus *Iphinoe* attained considerable numerical importance. This is not altogether surprising, for the Cumacea are normally bottom-living forms, but the appearance of one species (*Iphinoe fagei*, Jones) in considerable numbers in the plankton—exceeding 7000 in one haul at station WS 989—is of great interest.

The collections of Cumacea are confined to the stations relatively close to the coast, in shallow water. Evidently there is a succession of species from north to south. *Bodotria glabra* Jones occurred only in small numbers and only on the most northerly line of stations (19° 44′ S). On both the Walvis Bay line and Sylvia Hill line the two species of *Iphinoe*, *I. africana* Zimmer and *I. fagei*, were dominant in abundance. *Upselaspis caparti* (Fage) was present only off Walvis Bay and *Diastylis rufescens* Jones occurred only on the Orange river line.

The large catches of Cumacea occurred in the night hauls at stations WS 988 and 989, and *I. fagei* was the most abundant species. Jones notes that 'although the species present in these hauls may be able to live normally in the plankton, they show no special adaptations to this mode of life and their nearest relatives are coastal bottom-living forms'. Further, he says that when Cumacea have been caught in tow-nets at night, adult males have usually predominated, especially when attracted by artificial light, although in some recent records newly moulted adult or ovigerous females have outnumbered the males. In the hauls containing the largest numbers of specimens described here, both males and females of all stages were represented. These could possibly have been a nuptial swarm, but the following is a rather attractive alternative explanation.

It is interesting to compare these catches with a sample of the bottom fauna taken near Walvis Bay by Professor Spärk (1953). Here, in the belt of sand inside the anaerobic zone (p. 204), Spärk took 1910 Cumacea in a Petterson grab sample. Both stations WS 988 and 989 lay over the anaerobic zone, and if Spärk's specimens were the same species, *Iphinoe fagei*, then it seems reasonable to suppose that the great development of the anaerobic zone in March may have forced the Cumaceans up from their usual habitat on the sea-bed, to adopt a planktonic existence in the waters nearer the surface where oxygen would have been available.

The numbers of *Iphinoe* sp. corresponded closely with the distribution of the pilchard eggs and larvae (see p. 272).

AMPHIPODA

Although the amphipods have been separated from the samples, they have not been identified further, and it is only possible to remark on the total abundance of the group. They were present in relatively small numbers at all of the stations except WS 981. Their greatest abundance was at the offshore stations, where at WS 986, over 270, which appear to be mainly juvenile *Vibilia* sp., occurred in the 50–0 m. haul, but they were also present in moderate numbers at the inshore stations on the Orange river line. These *Vibilia* sp. appeared in numbers at stations where salps were also abundant, as was to be expected from the known commensalism between these animals.

EUPHAUSIACEA

Boden (1955) notes that fourteen species of euphausiids were represented in the collection from survey I. The numbers of adult euphausiids were quite small, but larvae of some species were numerous in some of the catches.

Nyctiphanes capensis Hansen was only taken at the stations on the continental shelf—excepting one larva which occurred in the 1000-750 m. haul at WS 997. It was present on all three latitudinal lines of stations. On the Orange river line the larvae extended farther seawards than the adults, but on the Walvis Bay line the greatest abundance of larvae—totalling 5000 specimens—occurred at WS 979, and this coincided with the greatest number of adults (twenty-seven) on this line.

The adults of *Euphausia lucens* Hansen, an oceanic species, occurred in very small numbers at the offshore stations, but a large haul of 237 adult females was taken in the 50-0 m. layer at WS 1000 on the continental shelf, and the adults were also present off the Orange river mouth (WS 1001 and WS 1002). The larvae were mainly abundant at the offshore station on the Orange river line (WS 996), but Barry (1956) in comparing Boden's material with some from New Zealand, questions the identification of these larvae as *E. lucens* and considers they may belong to some other species.

E. tenera Hansen, a tropical to subtropical form, occurred only at WS 996, at the offshore end of the Orange river line. Most larvae of this species were in the 250-100 m. haul. Boden is of the opinion that many of the unidentified pre-furcilia larvae encountered at other stations may in fact be *E. tenera*.

E. recurva Hansen, which occurred offshore on the Walvis Bay and Orange river lines, shows some suggestion of diurnal migration. *E. hanseni* Zimmer was represented by four adults in the 250-100 m. layer at stations WS 978 and 987 just off the continental shelf.

Of *Nematoscelis megalops* G. O. Sars mostly larvae were taken at the oceanic stations, and these, concentrated at about 250 m. during the day, show a diurnal vertical migration.

A species usually common in this area, *Thysanoessa gregaria* G. O. Sars, was present in very small numbers, well offshore.

Four species of *Stylocheiron* were also recorded.

DECAPODA AND STOMATOPODA

The collections of survey I have been examined and described by Dr M. V. Lebour (1954). Nearly all of the material consists of larval stages, but a few species are represented in adult form. A large number of genera and species were represented, but few were present in any abundance and the small number of individuals does not warrant a detailed account of their distribution.

Callianassa larvae were present at the inshore stations at Walvis Bay and on the continental shelf on the Orange river line. The phyllosoma larvae of *Jasus lalandii* (Lamark), the common crawfish of South Africa, were represented only by two specimens taken at stations WS 992 and 1000.

Among the Brachyuran larvae, a species of *Ebalia* occurred at both the offshore and shelf stations on the Orange river line.

Five adult specimens of the stomatopod, *Squilla armata* Milne-Edwards, were taken in a trawl in 128 m. of water at WS 990. Larvae of the same species occurred in ones or twos at the three inshore stations off Orange river mouth.

MOLLUSCA

The collections of planktonic molluscs have been reported on by Dr J. E. Morton (1954).

Specimens of the surface-living gastropod, *Ianthina ianthina* (Linnaeus) and *I. globosa* Swainson were taken by hand nets at two offshore stations (WS 1057 and 1058) on survey II. The heteropod,

Atlanta peroni Lesueur, a species common in subtropical Atlantic waters, occurred in small numbers at the offshore station on the Orange river line on survey I.

The pteropod *Limacina* was, however, numerically the most abundant mollusc in the collections. Two species occurred, the first *L. inflata* (d'Orbigny) only in small numbers at the offshore station WS 986. The other species *L. bulimoides* (d'Orbigny) also occurred at the same position, but was principally found at the offshore stations on the Orange river line. Here it reached great concentrations at the two stations WS 996 and 997. More than 3000 individuals were taken in the 250–100 m. haul at station WS 997.

We have seen (p. 229) that there was evidence of heavy grazing of the phytoplankton at these two stations and this may well be attributed to these enormous numbers of pteropods. Also present at these two stations were some specimens of the gymnosomatous pteropod, *Pneumodermopsis paucidens* Boas and its close association with the *Limacina bulimoides* and its probable feeding habits suggest that it may have been preying upon the *L. bulimoides*.

Two species of lamellibranch larvae occurred in the collections. Five hundred and forty individuals of larva 'A' were taken in the 50–0 m. haul at station WS 981 off Walvis Bay. The other species, larva 'B' was present off Sylvia Hill at stations WS 988 and 989 and more numerously off the Orange river mouth where 600 were taken at station WS 1002.

LARVACEA

The appendicularia from the samples, which include the genera *Oikopleura* and *Fritillaria*, have not yet been identified, but some remarks may be made on the distribution of the group as a whole.

Very large numbers occurred at the three inshore stations on the Walvis Bay line (WS 979, 980 and 981) reaching a maximum of about 5400 in the 50–0 m. haul at WS 980. The numbers fell off sharply, however, and only five individuals were present between 500 m. and 100 m. at station WS 978. At the stations seaward of this, modest numbers occurred in the surface-layers.

On the Sylvia Hill line of stations, a reversal of these conditions was observed. At the outermost station, WS 986, fairly large numbers occurred in all of the hauls. At WS 987 none of the hauls contained appendicularia. At station WS 988, large numbers (> 200) were again encountered in both the 50–0 m. and 100–50 m. hauls and at the station nearest the coast numbers decreased once more.

This distribution was nearly paralleled on the Orange river line, where virtually all of the appendicularia occurred at the two offshore stations. None was present inshore at stations WS 1000, 1001 and 1002. At the offshore stations numbers were highest in the surface-layers, and decreased with depth.

The explanation of this distribution is not easy without a more specific identification of the individuals. It may conceivably be the result of the presence of two separate populations of appendicularia —the first, in abundance inshore at Walvis Bay and extending southwards to WS 988 and 989 at the inshore end of the Sylvia Hill line, and the second, offshore on the Orange river line and Sylvia Hill line (WS 986) and extending northwards in decreasing numbers to the offshore end of the Walvis Bay line. Confirmation of this suggestion, will, however, have to await a more detailed examination of the species.

EGGS AND YOUNG STAGES OF FISH

Hart and Marshall (1951) have already commented on the fish-eggs and larvae which occurred in the plankton hauls. Of particular interest were the large numbers of eggs and larvae of *Sardinops sagax ocellata*, which occurred at the inshore end of all of the lines of stations, but particularly at the inshore stations on the Walvis Bay and Sylvia Hill lines. The greatest catch of 1000 eggs was taken in the

50–0 m. haul at station WS 989. Evidently spawning took place within 25 miles of the coast, in depths of about 50–150 m. A few post-larvae were taken in the deeper net hauls, but all were confined to the waters on the continental shelf. The heaviest catches occurred where the mean temperature of the upper 50 m. of the water column lay between 13° and 14·5° C. The importance of locating a spawning ground of this, the South African pilchard, is referred to on p. 270.

The eggs and young stages of other fish were also taken, notably those of the stockfish (*Merluccius capensis*), and of anchovies (*Engraulis* sp).

DISTRIBUTION OF THE ZOOPLANKTON

From the foregoing notes it is evident that there are many characteristic features in the zooplankton distribution, several of which might be expected from the known behaviour of the organisms. The ostracods, for example, are in this region an essentially mid-water group, lying off the edge of the continental shelf and showing a fairly well-defined distribution of species with depth, *Conchoecia elegans* being the dominant species and occupying the 500–250 m. layer. In the shallower waters, the role of the ostracods appears to be taken over by the Cladocera, which locally reached great abundance inshore on the Walvis Bay line.

The mysids were, on the whole, very poorly represented numerically, and only the one species, *Gastrosaccus sanctus*, which is normally particularly gregarious, attained any considerable numbers. This concentration occurred in the rather diluted water off the Orange river mouth. On the more northerly lines very few specimens were taken, and it is interesting to compare this with the abundance of cumacea at these more northerly stations.

The dominant cumacean, *Iphinoë fagei*, is closely related to other bottom living forms, and shows no particular adaptations to a planktonic existence. The large numbers occurring planktonically inshore on the Sylvia Hill line may be explained as being a nuptial swarm. But when one considers other phenomena—such as the presence of larval tubicolous polychaets with their tubes partly developed, the larval lamellibranchs with shells developed, and the post-larval Ophiuroids, all in the plankton—then one is more inclined to accept the alternative explanation, that the sea-bed of the anaerobic zone did not present a desirable environment and forced into the plankton many organisms which would otherwise have been present on the sea-bed at these stations.

The presence of the euphausiid *Nyctiphanes capensis* on the continental shelf is quite characteristic of its habit, and the other euphausiid, *Euphausia lucens*, only reached large numbers in the vicinity of the Orange river mouth, again in the shallow coastal waters. The close similarity in succession of species between the euphausiid fauna of this region, and that found off California, described by Boden, seems significant in view of the hydrological similarities between the two regions.

At the offshore end of the Orange river line the large numbers of the pteropod *Limacina bulimoides*, evidently grazing heavily on the phytoplankton (p. 229) and probably being preyed upon in turn by the gymnosomatous pteropod *Pneumodermopsis paucidens*, is the only major occurrence of the pelagic molluscs in the collection.

The distribution of the Larvaceae is strongly indicative of the presence of two separate populations, one in the coastal waters to the north, and the other in the oceanic waters to the south.

The association between the young amphipods (*Vibilia* sp.) and the salps, both of which occurred in numbers at the offshore end of the Sylvia Hill line, is no doubt an example of the well-known commensalism between these animals.

The correlation between the numbers of cumacea and the numbers of eggs and young stages of the pilchard is probably purely coincidental, but may be of some value since the cumaceans are fairly large and easily seen, and could perhaps be used as an 'indicator' for the pilchard eggs.

Taking the zooplankton as a whole, one gets the impression of a rather patchy and spasmodic distribution, quite large numbers of individuals of particular species occurring rather locally. This impression must, of course, be contributed to very largely by the fact that a relatively small number of stations cover a rather large area, but nevertheless there are few occurrences which suggest the population of specific water masses by particular organisms. The picture formed, in contrast to that created by the phytoplankton, rather suggests an independence from the more particular water masses, and an occupation by the animals of ecological niches more suited to their own habit than conforming to the circulation of the water masses. This applies in particular to the chaetognaths, whose distribution follows a similar pattern on all three lines of stations—*Sagitta friderici* occupying the water near the coast, with *S. serratodentata* a little farther offshore, and *S. decipiens* in the deeper water at the very edge of the continental shelf.

ECONOMIC RESOURCES OF THE BENGUELA CURRENT

FISH AND FISHERIES

In a region so organically rich as the Benguela current it is only to be expected that animals higher in the food chains and of more direct interest to man should also be found in abundance. In fact the pelagic fishes are already being increasingly exploited and among them the South African pilchard takes first place as the basis of extensive fisheries at various points along the coast. Following closely in importance are fisheries for the 'maasbanker' (*Trachurus trachurus*), stockfish (*Merluccius capensis*) and snoek (*Thyrsites atun*), and many sharks are taken principally for their liver oil.

It is clearly impossible, in a brief oceanographical survey, to obtain more than a glimpse of the fish populations and any account of these is more in the ambit of the Fisheries Division of the Department of Commerce and Industries in the Union of South Africa, which is conducting extensive research on this problem.

However, the inclusion of regional plankton sampling as part of the survey did reveal one point of major significance to the economic development of the region, and that is the discovery of an extensive spawning ground of the South African pilchard. As stated on p. 272 evidence was found of great concentrations of eggs and larvae near the coast in the vicinity of Walvis Bay and Sylvia Hill. It is not necessary, however, to enlarge on this here, for the details have been given in an earlier publication (Hart and Marshall, 1951).

Shellfish also have their place in the economic resources of the current, and there is a thriving fishery for the rock lobster (*Jasus lalandii*) on the coast in the southern part of the Benguela region. Although not yet developed, it is possible that squid may some day contribute to a fishery. Frequently large numbers of these animals were seen preying voraciously on saury pikes and lantern fish attracted by the lights of the ship when she was lying at the offshore stations.

SEALS

There are several herds of the Cape Fur Seal (*Arctocephalus pusillus*) on the west coast of South Africa. Their breeding-grounds extend from Cape Cross (21° 40′ S.) to Algoa Bay on the south-east coast, and established hauling-out places on the west coast are at Cape Cross, Hollam's Bird Island, several islands near and south of Luderitz Bay, at Kleinsee, Elephant Rock, and some more rocky islets near and south of Saldanha Bay (Rand, 1956). The places where the seals haul out are probably determined largely by the availability of suitable islets, and the topography of the coastline.

These seals are exploited commercially, and during the winter attention is focused on the yearlings of both sexes. During the summer, takings are limited to the bulls in certain rookeries.

WHALES

At the beginning of this century some experimental whaling was started in South African waters, and so encouraging were the initial reports that by 1912 some twenty-five companies joined in the quest from the Congo right round to the east coast (Olsen, 1915). Land stations were built, and on the west coast these have operated from time to time at Cape Lopez, Lobito Bay, Elephant Bay, Mossamedes, Port Alexandria, Tiger Bay, Walvis Bay, Luderitz Bay and Saldanha Bay.

Initially this whaling was based on the humpback whale. It appears, however, from the successes of various stations and the failure of others that the original theories concerning the migrations of the humpback up the west coast were open to question. An increasing amount of evidence suggests that the humpbacks, on their northward route from the antarctic, do not arrive at the Cape and progress steadily up the Benguela, but rather that they avoid the cold waters of the current and keep well out to sea, only striking the coast as far north as Portuguese West Africa. Blue whales, fin whales and sei whales are taken at Saldanha Bay, but rarely at the stations north of the Benguela current. Catches of sperm whales at Saldanha Bay have increased in recent years, but it appears that they are mostly found at some distance from the coast.

The small scale of the whaling in the Benguela waters suggests that the current does not form a particularly attractive environment for whales. This of course may be because the whalebone whales in these more northerly latitudes are seeking warmer waters for breeding rather than feeding. It is rather surprising, however, that there appear to be so few sperm whales in the Benguela current. The catches shown in the statistics are poor, and Townsend's charts (1935) also show that very few sperm whales were taken in the Benguela waters. Indeed, these charts showing sperm whales taken to the north of the Benguela, to the west in the south-east trade wind drift and to the south, create the impression that the sperm whale also must specifically avoid the cold coastal waters. These records of the varying intensity of whaling in different areas do not necessarily represent the density of the whale population, and they are coloured by the preference of the whalers for specific types of whale, but nevertheless they are strongly suggestive.

It is more difficult to interpret this avoidance of the Benguela current by the sperm whales than by the whalebone whales. The latter, we know, feed in the Antarctic, but for the former one might expect the rich waters of the Benguela to be an attractive feeding-ground. One can only presume that if the picture created by these records is correct, then there must be some other factor, such as the absence of suitable food organisms, etc., which makes the current unfavourable for the sperm whale.

GUANO ISLANDS

The fertile waters of the Benguela current, with their abundant stocks of fish, support enormous populations of sea birds. Practically every rocky promontory and island along the coast is densely inhabited by birds during the nesting-season. The relatively favourable climate with a markedly low rainfall has, in places where the topography has been suitable, led to considerable accretions of guano. Perhaps the most renowned deposits are found on the island of Ichabo (26° 17′ S.) about which an anonymous writer (obscurely described as ex-member of committee, 1845) quotes the following humorous poem:

> There's an island that lies on West Africa's shore,
> Where penguins have lived since the flood or before,
> And raised up a hill there, a mile high or more.
> This hill is all guano, and lately 'tis shown
> That finer potatoes and turnips are grown
> By means of this compost, than ever were known;

And the peach and the nectarine, the apple, the pear,
Attain such a size that the gardeners stare,
And cry, 'Well! I never saw fruit like that 'ere!'
One cabbage thus reared, as a paper maintains
Weighed twenty-one stone, thirteen pounds and six grains,
So no wonder Guano celebrity gains.

Attention was first drawn to the value of the deposits on Ichabo by Morrell (1852)[1], an American sealer. His earlier reports had been rapidly followed up, and by 1845 most of the guano had been removed from Ichabo and ships disappointed in their search there turned to the other islands and coastal deposits. Now, the utilization of the recent deposits is controlled, and for this purpose the islands are divided administratively and geographically into two groups: the 'northern group' comprising the islands to the north of Orange river mouth, and the 'colonial group' extending from 31° S. to the Cape.

Hutchinson (1950), in his monograph on vertebrate excretion, has dealt at some length with the South African deposits, and his work presents us with a very useful summary of what is known of them.

In both groups of islands there are three species of birds which make the major contribution to the deposits. These are as follows:

The Cape Gannet (*Morus capensis* Lichtenstein), (2) the Cape Penguin (*Spheniscus demersus* Linnaeus), and (3) the Trek Duiker (*Phalacrocorax capensis* Sparrman).

In addition to these three species it is probable that the other cormorants make minor contributions. These birds fulfil the principal biological attributes necessary for deposition of guano, in that they are colonial in nesting, and excrete at their nesting-sites. The best guano is formed where there is a minimum of extraneous matter such as sand and feather, etc. introduced into the deposit.

The guano, once deposited, is subjected to weathering, and it is through this process that the characteristic types of guano are developed. Rain and spray both wash the guano, and this results in the leaching of nitrogenous compounds from the deposit, producing the rather inferior *phosphatic* guano, with a low nitrogen content.

There is some evidence that the guano of the 'northern islands', which resembles the modern Peruvian guano, is relatively rich in nitrogen compared with the guano of the 'colonial islands'. The difference may be related to the higher rainfall in the 'colonial group' islands (e.g. Dassen island, see Fig. 3).

It appears that relatively flat islands, which are sufficiently high to allow deposition of guano well clear of the splash zone, form the most favourable substrate for successful accretion. The island of Ichabo in the 'northern group' is the richest producer, and some 2000 tons of guano are deposited there annually. From all of the west South African deposits about 10,000 metric tons are harvested annually, which can be taken as roughly equivalent to the annual deposition. Assuming an average content of phosphate (P_2O_5) of 10%, this would indicate an annual removal of about 440 metric tons of phosphorus from the sea in this region—an amount which would be equivalent to the complete removal of phosphorus from about $5\frac{1}{2}$ km.[3] of upwelled water. As the total volume of water in the Benguela current is probably of the order of 10^4 km.[3], the phosphate removed and deposited as guano must represent a very small part of the available phosphate in the upwelled water.

There is a certain amount of fluctuation in the total annual yield of guano and to some extent this may be related to the availability of food for the birds. In years of catastrophic mortalities of fish (see p. 199) there is some evidence of a fall in guano production, but such variations are by no means so pronounced as on the Peruvian coast. Perhaps this may to some extent be explained by the fact that the region most affected by these catastrophic phenomena is situated to the north of the islands, in

[1] The publication date of his narrative; his voyages took place much earlier.

the vicinity of Walvis Bay, and may only affect the northernmost guano islands. Other adverse phenomena such as abnormal meteorological conditions may have a more general effect over the whole region of the Benguela current.

REVIEW OF THE MAIN FEATURES OF THE BENGUELA CURRENT

The detailed description of the 'William Scoresby's' observations has presented a large number of facts and clearly, before advancing further, we must endeavour to bring these together to create a picture of the current as a whole.

Probably the most obvious feature of this, as of any other upwelling region, is the presence of water at the sea-surface many degrees cooler and incomparably richer in life than that normally found in the open ocean in the same latitude. On account of the temperature anomaly we find, as has been clearly demonstrated by the two 'William Scoresby' surveys, that the surface isotherms are disposed more or less meridionally in contrast to their latitudinal disposition over the greater width of the ocean. This is paralleled in the salinity distribution, and combines with the distribution of many of the other properties investigated in defining the entity of the Benguela current.

Within this general scheme a more detailed picture emerges, and one of the first things to notice is that nearly all of the physical, chemical and biological properties of the current exhibit discontinuity or irregularity both in time and in space. The Benguela current consists of a series of anticyclonic eddies, of interlocking tongues of cool and warmer water, of areas of rich and relatively poor phytoplankton, all of which merge into a complex pattern which is in a constant state of change or flux. This quality of irregularity and instability is in fact one of the features which emphasize the discrete character of this upwelling region.

In the 'William Scoresby's' two surveys there was a great contrast in conditions, and we have presented evidence to show that while in survey II, in spring (September–October), a state of active upwelling was encountered, on survey I, in autumn (March), the current was, at least in part, in a quiescent phase. One cannot be dogmatic about the criterion of normal conditions in such a region, but as the Benguela current is usually looked upon as a region of upwelling, we feel that there is a precedent for accepting conditions of active upwelling as being normal within the current and periods of quiescence as abnormal. It is in this light that we shall proceed to summarize the facts already presented and go on to consider the significance of upwelling in relation to the economy of the ocean as a whole.

NORMAL CONDITIONS

We have remarked on the greater activity of upwelling on the September–October (second) survey of the R.R.S. 'William Scoresby' and perhaps the first and most striking feature can be seen in the chart of surface isotherms (Fig. 7b). Here the low surface-temperatures inshore compared with those in the oceanic water to the west, and the configuration of the isotherms, gives one the impression of the cold water masses inshore driving actively out from the coast and thrusting out into the warmer oceanic waters.

This cool, low salinity water (Fig. 8b) moving offshore, clearly does not originate uniformly along the coast, but is produced in localized regions. In some cases these may be related to specific features on the sea-bed (Fig. 4), but in general it seems more probable that the dominating effect is that of the local winds in the particular areas. Our results have led us to deduce that while the trade wind far out at sea maintains a tension on the coastal water masses, the local diurnal winds are probably mainly responsible for producing an effective northwards along-shore or offshore drag on the sea-surface and supplying the energy necessary to create these localized centres of upwelling.

In the initial stages of upwelling the lighter surface-water must first be affected and removed away from the coast. To replace it, cooler and denser water must be raised from subsurface depths. This in turn will, however, be transported offshore, and where it meets the lighter surface-waters a relatively strong convection is set up. For example, on the Orange river line of stations the offshore waters are sharply separated from the cooler and denser upwelled waters by a pronounced convection cell (Fig. 37).

Evidently this sharp demarcation is present to a greater or lesser extent along the westward edge of the upwelling waters. The rapid alterations in temperature as this boundary was crossed (Fig. 9) throughout the region bear ample testimony to this, and so it appears that although no geographical boundary is present, the upwelled waters are in fact separated sharply from the warmer oceanic surface-waters lying to the west.

The upwelled waters have a lower temperature and salinity than the offshore surface-waters, and if one compares their T-S relationships with those at the offshore stations, it can be seen that they correspond to those at subsurface depths offshore (Fig. 33a) and while they undergo little or no mixing in the process of uplift, they are subjected to some degree of heating when they reach the surface. From this comparison we can determine the depth from which the upwelled water originates and this is seen to be in the layer between 200 and 300 m.

At this depth there is evidence of a subsurface current flowing southwards along the edge of the continental shelf, which we have termed the 'compensation current', and which appears to be the replacement source for water which is upwelled. In this respect it is interesting to note that the compensation current decreases in width in its southward journey (Fig. 34) as would be expected in a replacement flow.

In the waters of the compensation current the content of dissolved oxygen is extremely low and this can be attributed primarily to the source of the water in the oxygen minimum layer which extends over the tropical South Atlantic. Within the compensation current there is a gradual increase in oxygen content from north to south, probably on account of lateral mixing with the adjacent well-oxygenated oceanic waters. The significance of this low oxygen content will be the more evident in the next section of this paper (p. 279).

The waters of the compensation current, and those which are upwelled, have a relatively high content of dissolved inorganic phosphate phosphorus, and the entry of large supplies of this (and probably other) nutrient into the *euphotic* zone is of major importance to the biology of the region.

We have shown that in the coastal waters a large standing crop of phytoplankton was present. The main concentrations were found along the coast in the vicinity of the inshore end of the Sylvia Hill line (25° S.), where the numbers were made up by large quantities of *Chaetoceros* sp. and *Fragillaria karsteni* (at the station closest to the coast). In the warmer more saline oceanic waters, several species of solenoids, *Thallasiothrix longissima*, *Fragillaria karsteni* and *Planktoniella sol* were prominent in the phytoplankton, while in the vicinity of the boundary region the sparse flora contained elements of both the coastal and oceanic floras.

The results of survey II present us, therefore, with a picture of an actively upwelling region, extending in a belt some 80 miles wide along 1000 miles of the western coast of South Africa, an area within which the abundance of flora far exceeds that of the ocean to the west.

Abnormal conditions

On survey I in the autumn (March) we see similar general features, that is, cooler and less saline water along the coast, the eddy-like formation of the surface isotherms (Fig. 7a), etc., but in the more detailed features there is a marked contrast with survey II. This is most clearly seen in the vicinity

of Walvis Bay. Here the surface isotherms show a tongue of warm oceanic water pressing towards the coast, and influencing the region as far south as the Sylvia Hill line of stations (25° S.). The water masses on the landward side of this tongue are a mixture (Fig. 33 c, d), evidently derived from oceanic and coastal water types. The penetration of this influence to 25° S. creates in that latitude a reversal of the normal conditions, and there we find the apparent anomaly of warmer and more saline water lying along the coast, with the cooler and less saline water at the offshore stations (WS 986 and 987).

To the north of this wedge an extensive layer of oceanic water extended over the current, typically populated with a flora in which *Planktoniella sol* was a conspicuous member. In the southern part of the wedge, however, the flora was typically that of upwelled water, and inshore on the Sylvia Hill line (25° S.) and Walvis Bay line (23° S.) the largest quantities of chaetocerids encountered on the surveys were found.

It can be seen from Figs. 57 and 65 (pp. 225 and 231) that the highest concentrations of phytoplankton extended over a considerably larger area in survey I than in survey II. This was probably associated with the greater age of the upwelled water, but it may be that the greater stability of the upper water layers also enhanced its growth. In the offshore, unmixed oceanic water, the converse was true, and the phytoplankton there on the average was in fact four or five times less plentiful than on survey II. This may be associated with the more pronounced divergence of subsurface water which occurred seawards of the boundary on the second survey.

This great standing crop of phytoplankton, supporting a correspondingly large crop of zooplankton, must eventually sink down and die, and the nature of the bottom deposits is sufficient evidence that a very large part of the sinking and death takes place in the coastal region. The conditions prevailing at the time of the first survey would certainly have been conducive to this. The meteorological records show that there was little wind, particularly in the vicinity of Walvis Bay, and the currents appear to have been equally sluggish. Indeed, while the ship steamed across these waters, masses of moribund organisms, both phytoplankton and zooplankton, were encountered.

All this organic material sinking to the sea-floor decomposes fairly rapidly, and in so doing will both liberate nutrients and consume oxygen. That nutrients are released in some quantity is strongly suggested by the phosphate sections (Figs. 50–56) which show concentrations of phosphate in the waters of the continental shelf which exceed those in the water upwelling from greater depths. This local nutrient regeneration must play an important part in supplying the dense growth of plants with sufficient nourishment.

The removal of oxygen by decomposition has, however, less beneficial effects. So complete is this process that the water overlying the sea-bed of the continental shelf becomes completely anaerobic, and permits the growth of sulphate-reducing bacteria in the sediment. These bacteria, liberating hydrogen sulphide, enhance the effects of decomposition, and the hydrogen sulphide further reacts with the dissolved oxygen in the overlying waters.

We have already noted that the upwelling water originates from a layer of low dissolved oxygen concentration, and with the further removal of oxygen on the continental shelf it becomes still further depleted. In the normal conditions of flow of the current it does not become seriously reduced, as we can see from the oxygen sections of survey II (Figs. 41–44).

Presumably there is at these times a sufficient flow of water over the region to prevent stagnation. In abnormal conditions, however, the cessation of upwelling, and influx of warmer water on the surface, stopping or even reversing the current, has disastrous effects. These are demonstrated at Walvis Bay, on survey I, where the computed currents (Fig. 34) show a southerly flow in the wedge of oceanic water penetrating into the region, and where the section of dissolved oxygen (Fig. 40) shows that the oxygen depletion actually extended to the sea-surface inshore.

We believe that these events contributed, at least in part, to a small mortality of fish which occurred at Walvis Bay in March 1950. At times such mortalities assume catastrophic proportions (Brongersma-Sanders, 1948) and may seriously affect the fish stocks in this area.

Brongersma-Sanders (1948) has preferred to consider that the mortalities are due to poison originating from the discoloured water which is so frequently coincidental with mortalities. Some of the organisms causing such discolorations are known to be toxic to higher animals. The toxicity, of course, depends on the organism causing the bloom, and in the Walvis Bay region Dr Brongersma-Sanders suggests that a species of *Gymnodinium* may be the origin of such poisons. One of us (T.J.H.) has examined several discolorations or blooms in South African waters, and none of these were caused by that particular genus. *Peridinium triquetrum*, known to have predominated in some of them, has once been recorded in quantity coincidentally with a fish mortality in the Baltic (Lindemann, 1924), but it is a common dominant of polluted inshore waters so that its occurrence near Walvis Bay after a minor mortality might be the result rather than the cause of that phenomenon. This does not, of course, rule out the possibility that Brongersma-Sanders' hypothesis may be proved correct by further work, but from the existing evidence it seems to us more probable that the mortalities are caused by the coincidence of several unfavourable factors, one of which may be toxicity of bloom-forming phytoplankton organisms.

Not much more need be said about the animal populations. The collections of zooplankton have as yet only been analysed from survey I. They show a certain individuality in the general fauna of the current, but, as might be expected, the planktonic animals do not appear to show such a close correlation with the water masses as do the phytoplankton. Apart from this the 'William Scoresby' collections have provided some interesting material in connexion with the wider questions of the distribution of planktonic animals, a subject which lies outside the scope of this paper.

The abundance of the higher animals—the large populations of pelagic fish, seals and birds—and the presence of rich guano islands, are all characteristic features of upwelling regions and bear testimony to their productivity. The apparent scarcity of whales is seemingly anomalous but is perhaps an understandable exception (p. 275).

The discovery of a rich breeding-ground of the pilchard (p. 272) is yet another facet of this interesting region and it emphasizes the fact that many important features may yet be revealed by a more detailed examination of the region.

COMPARISON OF THE BENGUELA CURRENT WITH OTHER UPWELLING REGIONS

The features which we have described in the Benguela current have their parallel in other upwelling regions in the world, and in comparing these one is struck by the surprising similarity of the process and its attendant phenomena, in widely separate geographical localities.

Upwelling is characterized by a divergence of subsurface water masses towards the surface, and as such it is a widespread phenomenon throughout the oceans. By virtue of the effect of the earth's rotation on a current in the ocean the more dense water is found on its left-hand side (looking in the direction of flow) in the northern hemisphere, and on its right-hand side in the southern hemisphere. If the velocity of the current is sufficiently great, more dense (and consequently deeper) water will be lifted to the surface. This may occur along the edge of any suitable current, and may consequently occur either at a solid geographical boundary or at an oceanic boundary with another current. In the latter case we have examples in the divergences in the equatorial regions of the ocean, and in the former the divergences on coastal boundaries of fast-moving currents, for example the Agulhas

current. Such upwelling may vary with the velocity of the current independently of the winds, and we may distinguish it by referring to it as geostrophic upwelling.

On the other hand upwelling may be brought about by the direct influence of winds on the surface-waters, and it is into this category that the major upwelling regions of the world fit. This type of upwelling depends on the lie of the coastline and direction of the winds in relation thereto. It may occur at almost any time throughout the year (e.g. Peru, Benguela, etc.), but in certain regions of seasonal winds it may be a more restricted seasonal phenomenon (e.g. off south-east Arabia or the Indian coasts, Somali coast, Red Sea, etc.). The greater importance of this coastal upwelling derives from the greater depths which it affects. In geostrophic upwelling an upward tilt of isopycnals does occur, and the water brought to lie on the surface depends on the degree of tilt. In coastal upwelling, however, the isopycnals may be thrown up very steeply in response to the action of wind on the sea-surface and deep-lying density layers may be transported right up to the surface. In these conditions waters with a higher nutrient content are brought up to the surface, and the subsequent growth of life makes their presence all the more evident.

There are, as we have said, four *extensive* areas of coastal upwelling, all on the western coasts of the continents of North and South America and Africa, and it is in these that we may look for analogies and differences in the phenomenon.

These currents have certain visible features in common—a negative surface-temperature anomaly, characteristic coastal winds, frequent fogs over the cold water, and arid or desert conditions over the adjacent land. These phenomena, however, may be modified by the topography of the land. Thus, in South and West Africa, there is relatively low-lying land for some 80–100 miles from the sea; here the Namib desert occupies quite a broad strip along the coast, and the sea-breeze can develop a consider-able reach over the land. But in Peru the high Cordillera of the Andes is nearer to the coast; it confines the desert to a much narrower strip, and causes the coastal winds to blow more or less parallel to the coast and axis of the Cordillera.

There are also striking differences in the submarine topography of the various regions, which might be expected to influence the process of upwelling. Off South-west Africa the continental shelf is relatively broad compared with that off South America, where the steep slopes of the Andes are projected below the sea-surface to abyssal depths, with only a relatively narrow continental shelf. McEwen (1912) suggested that the upwelling off California showed a striking correlation between the areas of cold water and submerged valleys or other regions where the depth of the sea-bed increased rapidly with distance from the coast. Gunther (1936) could find no evidence of such a correlation off Chile and Peru, and the present work has indicated little or none off South-west Africa. Recently, Yoshida and Mao (1957) have constructed a realistic mathematical model of upwelling off California with little consideration for bottom-effects. There is, therefore, an accumulating amount of evidence which suggests that the actual process of upwelling may not be greatly influenced by the width of the continental shelf in these regions, although there may be effects on the attendant phenomena of the upwelling.

Essentially, the process of upwelling takes the same form in all of these regions. The discrete, eddy-like structure of the surface isotherms is common to all (Peru, Gunther, 1936; California, Sverdrup and Fleming, 1941; Morocco, Currie, unpublished), and the disposition of isopycnals suggests that the basic mechanism is similar in all cases, conforming to the pattern outlined by Sverdrup (1938). We have shown that the same basic mechanism probably occurs in the Benguela current (Fig. 37) and Gunther's density figures for the San Juan line off Peru suggest that a similar vertical circulation is present there also. It is a mechanism, however, which involves rather complex water movements in three dimensions. Fig. 96 may perhaps help to clarify them. It is based on our inferences as to the

water movements in the Benguela current, and is a diagrammatic and somewhat idealized version of them, but we feel that it is a fair representation of the circulation which is probably common to the major upwelling regions (but the mirror image of those in the northern hemisphere).

A striking feature of the Peru current is the very large apparent size of the anti-cyclonic eddies, which far exceed the dimensions of those found in the Benguela and California currents. There is some indication that these large eddies off Peru may conceivably have within them smaller eddies, but in themselves they appear to be peculiar to the Peruvian coast, and one can only assume that it must be constancy in the driving forces which enables them to persist and achieve such large dimensions.
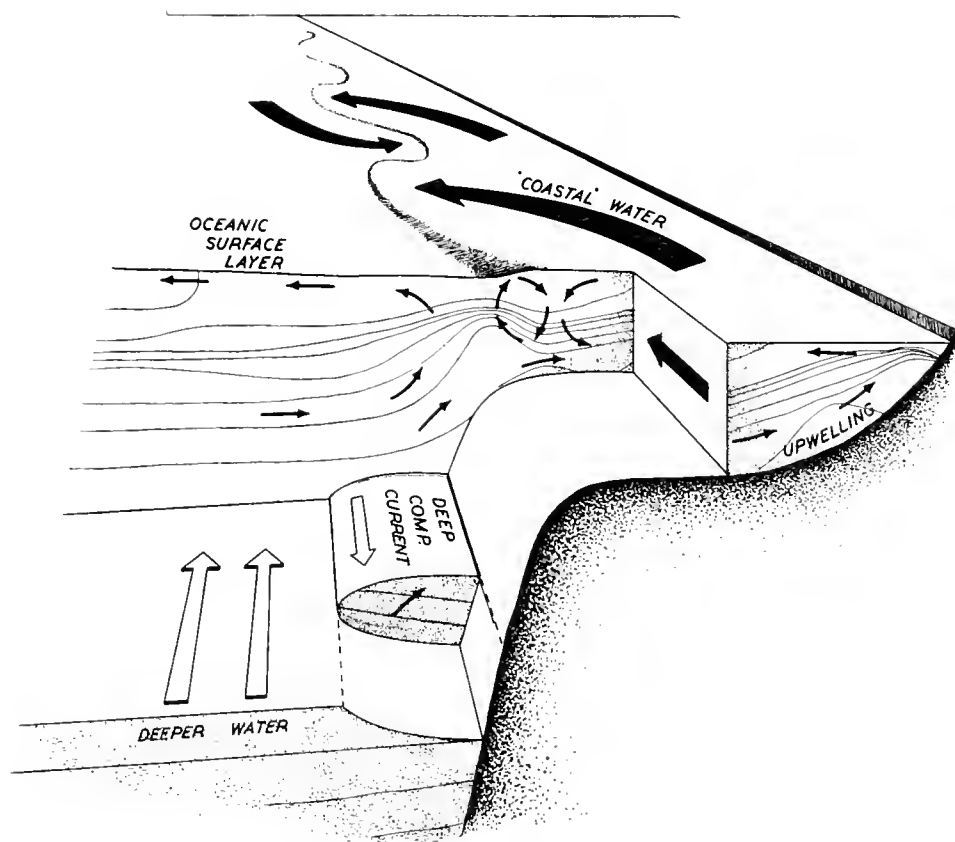

Fig. 96. A perspective diagram showing an idealized picture of the principal horizontal and vertical water-movements in the process of upwelling. The isosteres are represented by the thin lines on the 'cut' faces of the water masses. The shaded sinuous line on the sea-surface represents the continuation of the boundary convection between the upwelled and oceanic surface-waters. The name of the deep compensation current has been abbreviated.

The Peru current itself, of course, is very much more extensive than any of the other upwelling regions, for it runs along the South American coast for nearly 2000 miles. Furthermore it is unique in having within its range the subtropical convergence, and consequently involves subantarctic waters in addition to subtropical waters. By comparison the subtropical convergence in the South Atlantic lies well to the south of South Africa (Deacon, 1933). In spite of its great size, however, the Peru current has a slightly smaller negative temperature anomaly (-8° C.) than the Benguela (-9° C.), and both exceed by far that off California (-3° C.) and Morocco (-3° C.), (Dietrich, 1950).

Upwelling affects similar depths in all of these regions. Gunther (1936) quotes figures of 40–360 m. with a mean at 133 m. in the Peru current. Sverdrup (1941) states that in the California current upwelling was evidently confined to the upper 200 m., and in the Benguela current we have placed it at depths between 200 and 300 m. This removal of water from the 200–300-m. level appears to be accompanied in most cases by a subsurface compensation current. We have described this compensation

current below the Benguela current, flowing southwards and converging with the edge of the continental shelf and bringing water of low oxygen content southwards from the equatorial region. A similar current, better defined, is found off California (Sverdrup and Fleming, 1941) and also below the Peru current, although in the latter case the circulation is more complex. We have mentioned the inclusion of the subtropical convergence in the Peru current. At this convergence, subantarctic water sinks and flows northwards along the coast below the warmer subtropical waters. Off the Peru coast one can identify the southward flowing compensation current, but in 20° S. it meets the northward flowing subantarctic water and is forced under the latter but continues to flow south. A salinity maximum and the low oxygen content are also identifiable to at least 35° S.

The outstanding feature of these compensation currents is their low oxygen content, which in the Benguela current is traceable to the origin of the water in the minimal oxygen layers of the equatorial parts of the oceans. Sverdrup and Fleming (1941) have shown that a further reduction of oxygen takes place with the local decomposition of organic matter. Off the California coast the level of the oxygen minimum lies at a greater depth than off Peru and South-west Africa. Water with an oxygen content of less than 1·0 ml./l. was rarely found at depths of less than 250 m., even at the inshore stations off California, whereas both in the Peru current and Benguela current upwelling brings the low oxygen water up on to the shallower reaches of the continental shelf.

It is clear that there are very close similarities between the abnormal conditions found off South-west Africa, and the 'Callao Painter' and 'Aguaje' off Peru. At the north end of the Peru current periodic incursions of warmer water invade the region where cool upwelled water is usually present. These are referred to as the 'El Nino' current, and Gunther (1936) states that 'one finds in place of the cool Peru Current diverging from the shore, hot poorly saline water of the Equatorial Counter Current flows southwards and converges with it. The rise in temperature kills fish and plankton which then decompose and emit sulphuretted hydrogen on an enormous scale. This is the Callao Painter...'. While the 'Callao Painter' or 'Aguaje'[1] occurs in conjunction with the 'El Nino', it can also be associated with the convergence of warm oceanic water with the coast, and in this respect we find a close parallel with the conditions off Walvis Bay on survey I.

We have expressed the opinion (p. 199) that the low oxygen content of the upwelled water, accentuated under conditions of stagnation or reversed flow of the current, must be a very important factor in the catastrophes off South-west Africa. The coincidence of low oxygen and the manifestations of the Callao Painter is strongly suggestive of a similar sequence of events off the coast of Peru (Burtt, 1852; Currie, 1953 b).

Perhaps it is significant in this respect that records of pronounced abnormal conditions and fish mortalities are rare on the California coast, where the low oxygen water does not normally appear to be elevated to the proximity of the sea-surface on the continental shelf.

The frequency of records of green diatomaceous mud from the Peru coast (Neaverson, 1934) lend further support to the theory that conditions on the sea-bed of the continental shelf must be virtually anaerobic. Otherwise the chlorophylls and associated pigments would be oxidized to give the sediments a brownish or grey appearance.

Deposition of diatomaceous mud occurs at a much greater depth off Peru than off South-west Africa. Off South-west Africa the diatom mud occurs principally between depths of 50 and 150 m., though it extends to greater depths at the landward end of the Walvis Ridge. The sediments in the deep water beyond the continental shelf are mainly globigerina ooze. Off Peru, however, Neaverson

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[1] Evidently some confusion attends the use of the name 'Aguaje'. In the New Velasquez Dictionary it is defined as 'A current in the sea, persistent or periodical; e.g. the Gulf Stream'! Dr Wooster points out to us his impression that 'Aguaje' used in Peru refers to discoloured water of biological origin, only occasionally associated with the 'Callao Painter'.

(*op. cit.*) records diatom mud in abyssal depths; it is usually brown, but sometimes retains a greenish appearance (WS 694, 1216 m.). Tentatively one may ascribe this deposition in deep water to the lesser width of the continental shelf off Peru. The persistence of a green colour of organic origin in these very deep water sediments in the Peru Basin is more difficult to understand, for the sediment must be deposited through water which is fairly well oxygenated.

ORGANIC PRODUCTION IN THE BENGUELA CURRENT

The 'Willlam Scoresby's' surveys were aimed at obtaining a more detailed picture of water-movements and plankton distribution in the Benguela current than had hitherto been available. What we have obtained, therefore, is a more or less instantaneous picture of what was taking place on the two surveys. Such limited observations, particularly in a region of such great variability, can tell us little about such a complex process as organic production. We can, however, say something of the biological activity which was taking place in the particular water masses and from this obtain some idea of how the biological processes within the current compare with those in the adjacent oceanic waters.

On the second survey the greatest quantities of phytoplankton were taken close to the coast between 24° and 26° S., in an area where active upwelling was taking place. Further offshore the quantities decreased, and this suggests that the most favourable conditions for the proliferation of the phyto-plankton were present in the very (nutrient) rich, cold water entering the euphotic zone. The upwelling water enriched by the local regneration must have had a very high concentration of dissolved inorganic phosphate-phosphorus, and even this profuse growth of phytoplankton had only reduced it to levels still above 1 mg. at $P/m.^3$. Further seawards, phytoplankton and phosphate both decreased.

In the oceanic surface-water offshore there was a secondary increase in the quantity of phyto-plankton, but the amount of phosphate continued to decrease. Qualitatively, however, this offshore phytoplankton was different from that inshore, being dominated by panthalassic or more definitely oceanic species—some of the solenoids in particular for which no doubt the oceanic environment, enriched by lateral mixing from the coastal waters and perhaps also by some divergence seawards of the boundary (see Fig. 96), presented most favourable conditions.

It seems, therefore, that on survey II we have a situation analogous to that described by Sargent and Walker (1948) in the California current. There they found the richest population, dominantly chaetocerids, in the recently upwelled water. From this there was a succession, in the eddies of upwelling water, to a rather sparse warmer water flora in the upwelled water which had been in the surface for the longest time. On survey II in the Benguela current, the eddies were not so far developed, and what we have reported may be a compression of the succession indicated by Sargent and Walker, between the coast and the boundary region, with a separate and distinct oceanic flora to the west of the boundary.

On the first survey, in autumn, the quantity of phytoplankton in the oceanic water was considerably less, by four to five times, than in spring, but there is some evidence that at least in places it may have been richer shortly before the survey was made. At stations WS 996 and 997 the very marked phos-phate depletion in the surface-layers, with the presence of a large number of pteropods and numerous faecal pellets, suggests that the low crop of phytoplankton may recently have been much greater and had since been reduced by heavy grazing by the pteropods.

In the coastal waters, however, in the relatively abnormal conditions of the autumn survey (I) the average numbers of phytoplankton were greater than in spring, and the area of high concentration extended farther from the coast. Chaetocerids again dominated in the richest region but not all of the dominant species were the same. Many more *Asterionella japonica*, *Eucampia zoodiacus* and

Stephanopyxis turris were present than in spring. One noteworthy feature is that the richest stations on survey I were found in the coastal waters between 23° and 26° S. where the effects of heating and mixing with more saline water were clearly recognizable. Even amidst this dense flora, relatively great quantities of phosphate were recorded. In this area, as we have noted, many moribund plankton organisms and lines of foam, probably accumulations of dying phytoplankton, were observed on the sea-surface, and the conditions would, therefore, have been conducive to a rapid regeneration of nutrients from the decomposing plankton (Seiwell and Seiwell, 1938). Many resting spores of *Chaetoceros didymum* and *C. subsecundum* occurred in the plankton samples, but we have insufficient data to decide whether these were associated with such conditions or merely exhibit the seasonal change in autumn.

The development of the peak population under such conditions is not altogether surprising, for even with uninhibited exponential growth it must take some time for diatoms to reach such dense concentrations in a newly upwelled water mass, and on this occasion the greater age of the upwelled water and higher temperatures would have favoured such a development.

On both surveys the contrast between the densities of the coastal and oceanic populations of phytoplankton was an outstanding biological feature of the region. It should be specially noted that on survey I the coastal populations reached a figure some *four orders of magnitude* greater than those in the oceanic waters, and on survey II the range was three orders of magnitude. The actual figures are given in Tables 14 and 15 (pp. 224 and 230), and their distribution in Figs. 57 and 65 (pp. 225 and 231).

Even the crude settlement volumes of the net hauls (Tables 14 and 15) suffice to show that the rich inshore phytoplankton of the Benguela current is roughly comparable in quantity to that found in the Peru current (Gunther, 1936) and in the more oceanic waters of the antarctic zone during the main increase (Hart, 1934, 1942). They are significantly poorer than those found in northern antarctic coastal waters (South Georgia) in late spring, but much richer than the values recorded there during the post-maximal decrease and in winter. In the Benguela coastal waters there seems to be but little seasonal falling off in quantity so long as the surface-layers are replenished by upwelling, so that it is quite probable that the total annual production there equals or even exceeds that of the South Georgia area, though the latter (at the height of the spring increase) can amount to 7–10 times the Benguela or Peru averages. These figures from South Georgia in fact furnish by far the greatest standing crop values yet known to us from any part of the world.

The open ocean, we know, presents a relatively stable and uniform environment and this in turn appears to be accompanied by stability in the biological processes occurring in these waters. On the other hand, the dominant physical feature of upwelling regions is their irregularity even under normal conditions and this is paralleled with a constantly changing biological picture.

Unfortunately our knowledge of the upwelling process is still far from being quantitative and until we can measure the processes of advection, eddy diffusion and mixing in the upwelling water we can go no further than to describe a very generalized picture of the environment and conjecture about the processes occurring therein.

Nor do the biological phenomena lend themselves to ease of measurement, continually undergoing rapid and extensive fluctuations. Steeman-Nielsen and Jensen (1957) have shown how the high-standing crop of phytoplankton is accompanied by a high rate of primary production. The transfer of organic matter through the organic cycle is initially dependent on the grazing of the herbivorous animals, and the success of the transfer depends on the efficiency of the grazing process. The high-standing stock of higher animals in the area shows that the extent of the grazing must be very great. Nevertheless plants which are not eaten eventually sink, die and decompose, and in the bottom deposits

of the South-west African region there is evidence that sinking and death of the phytoplankton occurs on a large scale. This, together with the ephemeral nature of the upwelling, leads one to question the efficiency of the grazing and to suppose that it may not reach its potential level, and that much organic matter may be lost at this early stage in the organic cycle.

It is tempting to speculate on the possible interactions of primary production, sinking and grazing in a region such as this, but our data do not permit us to put any time-scale on the processes involved and so at best such a discussion would be truly speculative. Clearly this would be one of the prime considerations in any more extensive a study which might be contemplated in the future. It is quite outside the scope of an exploratory survey such as was made by the 'William Scoresby'.

SUMMARY

The R.R.S. 'William Scoresby' made two surveys of the waters off the South-west African coast as part of a more extensive programme of oceanography and whale-marking in the Atlantic and Indian Oceans.

These surveys, the first in autumn (March) and the second in spring (September–October) 1950, were planned to obtain a more detailed picture of the water movements and biological features of this region than had hitherto been attempted. Furthermore, the comparison of this region with the Peru coastal current which had at an earlier date been surveyed by the same ship and with other upwelling regions was one integral part of the wider field of work, the study of organic production in the oceans.

The report commences with a brief account of the early voyages and previous scientific work in this region, notably referring to the work of the 'Meteor' expedition, 1925–7, some of whose observations were made in South-west African waters.

The oceanographical methods used on these surveys are described together with the various laboratory techniques and methods of analysis which were later used in interpreting the observations. This section on the work of the R.R.S. 'William Scoresby' is concluded with a detailed account of the itinerary of each survey.

A description of the topography of the coastal region of South-west Africa and the adjacent sea-floor follows. An outstanding feature of the coast is an extensive arid desert, the Namib desert, whose existence is intimately connected with the presence of cool surface-waters along the coast. On the sea-floor, the continental shelf has a width of some 40–80 miles and from the edge the bottom slopes away steeply into the abyssal depths of the Cape and Angola basins. These basins are separated by the Walvis Ridge, a prominent feature which connects the continent of Africa to the Central Atlantic ridge.

The wind system over the south-west African region is shown to be divided into two well-defined components, the south-east trade wind which predominates over the oceanic waters and the diurnally variable coastal winds which prevail in a belt extending seawards some 80 miles from the coast. The trade wind can be considered as the eastern limb of the anti-cyclonic circulation of air over the South Atlantic and the coastal winds as a divergence of the coastal boundary of the trade winds, resulting from the extensive diurnal pressure changes over the continent. The coastal wind of importance is S.S.W., which brings warm, moist air from the ocean over the cool coastal waters, and leads to the formation of fogs and the aridity of the land to leeward.

During the surveys, the trade wind was weaker in March (survey I) and better developed in September–October (survey II). The coastal winds were on the whole weak in March and stronger in September–October.

The sea-surface currents are, like the winds, divisible into two clearly defined circulations. In the

region of influence of the trade wind, a N.N.W. flow is induced and this forms the eastern limb of the anti-cyclonic circulation of the South Atlantic. Nearer the coast and sharply demarcated from this drift, the currents are variable, and as the oceanographical observations show, are characterized by pronounced vertical movements. We have restricted the use of the name Benguela current to this coastal circulation in which the upwelling movements occur and have referred to the oceanic circulation as the 'south-east trade wind drift'.

The distribution of temperature and salinity of both surveys has shown that these two currents are characterized by two different types of water—the coastal or upwelled water, and the oceanic water which is warmer and more saline. Varying mixtures of these two types occurred in some areas.

A comparison of the two surveys showed that while in September–October (survey II) active upwelling was taking place over most of the region surveyed, in March (survey I) the waters were more quiescent and a large part of the coastal region was occupied by an influx of mixed oceanic water.

The relationship of the water masses in the south-west African region to those in the South Atlantic as a whole is discussed at some length, and it is evident that the cool, less saline coastal waters are derived from the South Atlantic central water at subsurface depths (200–300 m.) offshore.

A computation of the dynamic height anomalies of the sea-surface relative to the 600 db. surface agrees essentially with the deduced water-movements and emphasizes the eddy-like nature of the coastal circulation. The topography of the 200 db. surface (relative to 600 db.) depends on rather few observations at this depth, but indicates a southerly flow along the edge of and converging with, the continental shelf. It is suggested that this is a replacement flow for the water which is upwelled, and it has been termed the 'compensation current'.

The mechanism of the upwelling has been examined, and it was found to be essentially similar to the process off California described previously by Sverdrup (1938). Where the upwelled waters of the Benguela current meet the warm oceanic waters a convection cell develops, which forms a sharp boundary, and the position of this, although variable, lies some 40–80 miles offshore, in the vicinity of the edge of the continental shelf and the position of divergence in the surface wind system.

The distribution of dissolved oxygen in the subsurface 'compensation current' suggests that the latter is continuous with the oxygen minimum layer in the equatorial parts of the ocean, and may indeed arise from the latter. The impoverishment of oxygen in this water which is evidently the source of the upwelling water, is further accentuated by the decomposition of organic matter on the sea-bed of the continental shelf, and in certain areas anaerobic conditions are created where sulphate-reducing bacteria thrive and liberate hydrogen sulphide into the overlying waters. In March (survey I) the depletion of oxygen extended to the sea-surface inshore at Walvis Bay and we believe this may have contributed to a small mortality of fish which occurred at Walvis Bay during the survey. The association of this phenomenon with the incursion of mixed oceanic water and calm conditions at Walvis Bay suggested a correlation between the fish mortalities and such conditions, and examination of earlier records of winds, strengthens the correlation between mortalities and calms or northerly winds in this area.

The considerable amount of decomposition of organic matter taking place on the sea-bed of the continental shelf led to a further enrichment of the already phosphate-rich upwelled water.

On survey II an attempt was made to determine the total extent of the anaerobic or 'azoic' zone on the sea-floor of the continental shelf. This was found to extend, at least in patches, for a distance of 400 miles along the coast.

The terminology used in the account of the microplankton and the taxonomy of the main groups met with during the two surveys are discussed at length. Part arbitrary groupings, devised solely to aid presentation of these data, are also described in detail. Drastic changes in the accepted practice in

the literature of the subject over the last few years seem to make this essential. For the same reason full notes are given on recent changes in taxonomy of certain individual species better known under earlier names.

The diversity of the microplankton is demonstrated by the full list of all microplankton categories recognized during the routine analyses, and tabulation of the records of frequency of occurrence and of dominance.

The next two subsections deal with the distribution of the main groups of the microplankton, and in particular the distribution of the dominant group, the diatoms; arrayed according to the grouping devised for this purpose. The two surveys are treated separately with the aid of diagrams and tables. This shows that the general pattern of distribution of the more important microplankton species conformed fairly closely to the disposition of the water masses.

In the rich upwelled coastal waters chaetocerids were dominant, with certain markedly neritic species from the other groups (e.g. *Stephanopyxis turris*, *Eucampia zoodiacus*, *Fragilaria karsteni* and *Asterionella japonica*). The extent and average intensity of the rich inshore phytoplankton were greatest during the first (autumn) survey, though the heaviest individual hauls were obtained in spring. Forms such as *Planktoniella sol* and *Thallassiothrix longissima* were typically dominant in the much sparser phytoplankton of the offshore waters, together with certain solenoids during the second survey. The transition zone, which seems nearly to coincide with the hydrologically determined divergence region, usually contained a scanty microplankton consisting mainly of more panthalassic types from either of the main habitats.

The more extensive coastal production in autumn (survey I) with numerous resting spores of the dominant chaetocerids is thought to represent a late stage in the succession of waters earlier enriched by upwelling, since that process was proceeding but weakly at the time. Probably this is not a purely seasonal effect, for upwelling probably persists, intermittently, throughout most of the year. Hence the succession may be repeated several times annually. During the spring survey (II) the rich coastal area was narrower, and the proportions of the dominant species rather different, with few resting spores. Upwelling activity was great, as shown by marked instability of the surface-layers among other hydrological features. Here an early stage in the probable succession is postulated, some of the enriched water having risen to the euphotic zone too recently for the phytoplankton crop to have taken full advantage of it. Attention is drawn to the analogy with conditions observed in the California current by workers benefiting from more complete seasonal coverage (Sargent and Walker 1948).

Conversely, the scanty offshore phytoplankton was much richer during the spring survey than it had been during the autumn. Here it seemed that the increased turbulence occasioned by greater wind stress was proving definitely beneficial to plant production.

In the section on special distributional features, species have been selected whose distribution in the routine hauls seemed best to illustrate either the general distributional trends or divergence from the pattern typical of the group to which they belong. Their distribution is described and charted in detail.

Observations on visibly discoloured sea-water within the area surveyed confirmed that the dark green to opaque black appearance of large areas near Walvis Bay was due to the dense population of inshore diatoms, as Gilchrist (1914) had previously recorded. *Chaetoceros didymum* and *Asterionella japonica* were two of the species mainly responsible. Within this same area more localized brownish discolorations were also seen, and three samples from these showed the development of a definite 'bloom' of *Peridinium triquetrum*, with lesser numbers of *Prorocentrum micans* and diatoms, sometimes associated with lanes of salps and ctenophores dying at the surface. A minor fish-mortality had occurred near Walvis Bay just before. Detailed analyses of these samples are given, and their possible significance in relation to mortality phenomena discussed.

On the second survey one intense red discoloration was seen close inshore in the extreme north of the area, which was found to be due to the ciliate *Cyclotrichium meunieri* Powers (= *Mesodinium rubrum* Lohmann) and its associated symbiotic alga. This is discussed in relation to previous observations of it round Cape Province, and recent revisions of the taxonomy.

A rearrangement of the data concerning the main diatom groups, based on arbitrarily selected distance limits, illustrates the distinction between offshore and inshore diatom floras, and provides some basis for ecological characterization of the species within each of the groups, somewhat on Gran's lines.

This concept is carried a stage further in an attempt at 'ecological characterization' of the more important plankton diatom species of the area. Comparison with their recorded distribution elsewhere shows that they are even more cosmopolitan than was generally recognized hitherto. This lends point to the argument that it is the relative importance of the various forms, rather than their mere presence and absence, that must be studied before the relations between marine plankton floras and their 'conditions of existence' begin to be perceptible. In this there seems to be a basic contrast between the planktonic floras and faunas, for 'presence or absence' is often of real significance in the latter.

The zooplankton has been completely sorted only from survey I. Some groups have been reported on and the findings of these are summarized. The outstanding feature of the zooplankton distribution appeared to be its greater independence of specific water masses than the phytoplankton and a conspicuous patchiness in the distribution of some species.

A brief account is given of other life in the current—notably the fish, seals and whales, and also the guano islands, all of which are outstanding economic features of the region.

Reference is made to a spawning ground of the South African pilchard, located between Walvis Bay and Sylvia Hill. This is a point of some importance but has been dealt with in a separate publication.

Many features of the Benguela current are similar or analogous to those of other upwelling regions and a concluding section is devoted to comparing the main features of the four major upwelling regions of the world. The extraordinary richness of upwelling regions in comparison with the adjacent oceanic waters presents interesting material for speculation on the process of organic production in these environments. At present, however, our knowledge of the magnitude of the processes does not permit any quantitative treatment of this problem.

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THE APPENDAGES OF THE HALOCYPRIDIDAE

By

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INTRODUCTION

A PROLONGED systematic study of ostracods has impressed me with the remarkably constant pattern of the structure, even to the fine details of setation, of the appendages of the Halocyprididae. In earlier literature (Müller, Claus, Sars, Vavra), brief descriptions of the anatomy of these animals are to be found, but they usually refer only to isolated limbs or to the carapace. More recently Skogsberg (1920, 1946) has given minute details of the structure and setation of appendages in a number of species, but nowhere is there a description of the anatomical and spatial relationship of the various limbs to each other. This is essential to the proper understanding of the functional morphology, the way in which the limbs are used, which, in its turn, is essential as a background to further advances in the study of the taxonomy and thus the evolution of the group. The following paper is an attempt to supply this deficiency.

The family Halocyprididae is included in the Myodocopa, which is characterized as follows: shell generally with an antennal notch; seven pairs of appendages; frontal organ usually present; antenna biramous with well-developed propod, exopod multiarticulate and bearing natatory setae, endopod normally small and often prehensile in the male; mandibular palp pediform; caudal furca with lamellar rami bearing marginal spines. All the members of the Halocyprididae are planktonic and have appendages adapted to this mode of life.

Although numerous species have been studied during the course of my work, one was selected for intensive study, namely *Conchoecia borealis* G. O. Sars var. *antipoda* G. W. Müller, not because it is more typical of the group than any other species, but because material fixed in alcoholic bouin was available in the Discovery collections. This had been very kindly handed to me by Professor H. Graham Cannon. The material was suitable for cutting wax sections which could be used to check certain features of anatomy. Formalin-fixed material also available from the Discovery collections was unsuitable for embedding in wax. It was used, however, for the preparation of thick celloidin sections for study by methods similar to those described by Professor H. Graham Cannon (1933). The greater part of my work on the group, however, has been carried out by the use of fine or microdissection methods. After removing the carapace, antennules and frontal organ, the remaining appendages of the left side of the animal were separated by cutting the arthrodial membranes by which they articulate with the body. By this means, not only could an independent study of the isolated appendages be carried out, but the body of the same animal could be mounted left side uppermost. With sufficient care in dissection, the relationship of the inner faces of the undisturbed appendages of the right side could then be studied. In preserved material the appendages occupy a range of positions which must represent those which they could take up during life. Study of a number of such specimens and the articulation and musculature of their appendages has been of value in interpreting the observations of live animals made by Müller (1894).

Müller (1906), whose figures were quoted by Skogsberg (1920), gave a very wide distribution for

Conchoecia borealis antipoda, between 1° S. and 65° S. in the Atlantic Ocean at depths of 470–1600 m. The Discovery specimens used for study were taken at stations 138, 529, 661, 662 and 671 which ranged from 43° 08′ S. to 57° 36′ S. From the data provided by the samples taken with closing nets the specimens would appear to have been captured at depths greater than 250 m. to below 1000 m. The species would appear to be a deep-water form.

Müller (1906) regarded *Conchoecia borealis* and *C. antipoda* as separate species, but Skogsberg (1920) stated that the differences between them were too small to merit greater rank than that of a variety. Both authors found the females to be larger than the males; the Discovery specimens bear out this difference in size. Skogsberg (p. 718) also found 'that the shoulder-vault had a sharp edge contrary to what is stated by G. W. Müller 1906', both males and females being alike in this character. In the few males examined from the Discovery collections the shoulder-vault was sharp-edged but not quite so far expanded as in the females. Skogsberg described the setation of the appendages in great detail, but some repetition and further discussion has been found necessary in this report.

The intensive study of *C. borealis antipoda* leads on to a comparison with other halocyprids, e.g. *Archiconchoecia*, *Euconchoecia* and *Halocypris* and to a comparison of this group with the Cypridinidae.

ACKNOWLEDGEMENTS

THE APPENDAGES, THEIR INTERRELATION AND FUNCTION
ANTENNULES (Figs. 1 and 2)

The antennules are uniramous and exhibit sexual dimorphism. Their shafts articulate antero-dorsally with the body of the animal, close beneath the hinge of the carapace. They are normally directed straight forward.

In the male (Fig. 1 B) each is rigidly bound to the long slender shaft of the frontal organ by a single pair of inner dorsal hooked seta. The three terminal setae are of great length. Of these latter, the principal and one of the secondary setae bear an armature of spines and setules, which lock them together for part of their length. Only the apices diverge. This armature differs in other species and is a specific character of differential value. The setae are directed forward and slightly downward through the anterior gape of the carapace. By flexure of the apical articles of the antennule, they can be folded back and beneath the animal, between the bases of the appendages. Besides the principal and secondary seta there are two so-called 'tube-setae' near the apex of the antennule. These are much shorter than the principal setae, stout, bluntly ending and very thin walled.

In the female (Fig. 1 A) the shafts of the antennules are not locked to the frontal organ. The inner dorsal setae extend forward to just beneath the rostrum. A single apical seta, corresponding to the principal seta of the male antennule, is extended forward and downward, but its length is such that it extends only slightly beyond the margin of the carapace (Fig. 2, a_1s). The secondary setae of the female are similar to the sensory tube-setae of the appendage of both sexes. In both sexes these terminal tube-setae are carried hanging downward within the anterior gape of the carapace.

It would seem that in the halocyprids the function of these appendages is largely sensory, though there is no experimental evidence of this. The thin-walled tube-setae are of a type similar to other 'chemo-sensory' setae found in the Crustacea. They lie directly in the path of the water-current flowing through the carapace, because they hang vertically in its anterior gape. The principal setae,

as already mentioned, show sexual dimorphism and specific variation in their armature, and may have some special secondary sexual function. The fact that in some species, even in the male, their free tips have a structure similar to the sensory tube-setae may mean that they also are sensory.
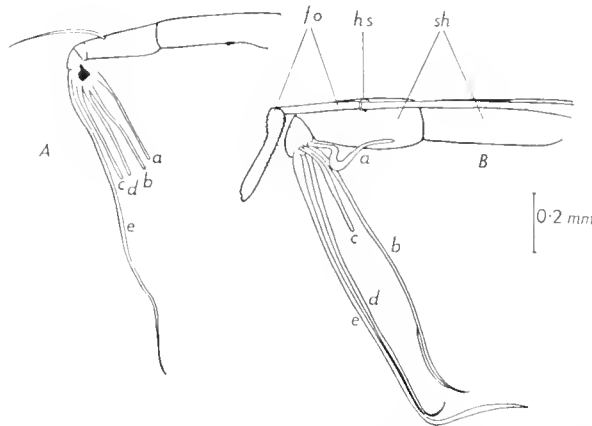

Fig. 1. *Conchoecia borealis antipoda*. Right antennule from inside. A, female; B, male with frontal organ. *f.o.* frontal organ; *h.s.* hooked seta; *sh*, shaft; *a* and *c*, tube setae; *b* and *d*, secondary setae (tube setae in female); *e*, principal seta.
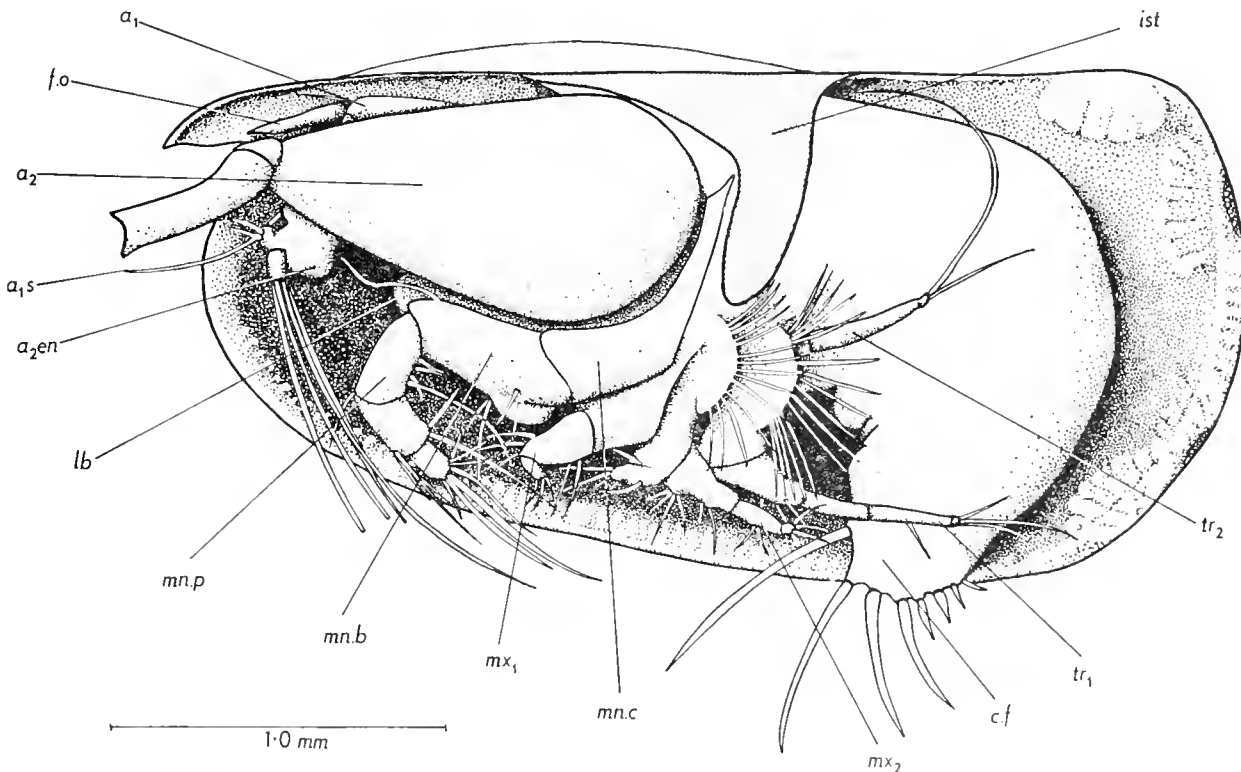

Fig. 2. *C. borealis antipoda*. Female with left valve of carapace removed, antennal exopod omitted. a_1, antennule; a_1s, principal seta of antennule; a_2, antennal shaft; a_2en, antennal endopod; *c.f.* caudal furca; *f.o.* frontal organ; *ist*, isthmus linking body to carapace; *lb*, labrum; *mn.b.* mandibular basis; *mn.c.* mandibular coxa; *mn.p.* mandibular palp; mx_1, maxillule; mx_2, maxilla; tr_1, first trunk limb; tr_2, second trunk limb.

ANTENNAE (Fig. 2, a_2, Fig. 3)

The antennae are biramous with the exopod composed of eight or nine articles and the endopod small with not more than three articles. The endopod shows sexual dimorphism. As in most Myodocopa, each relatively enormous, broadly expanded shaft contains a powerful musculature. Each articulates

antero-laterally with the body just behind the antennules and extends straight forward. The multi-articulate antennal exopod with its long natatory setae is similar in both sexes. It articulates somewhat to the outside of the apex of the shaft, the articulation corresponding exactly in position with the base of the antennal notch of the carapace (Fig. 2). It can be extended through this notch or withdrawn into the carapace and then lies beneath the body of the animal, with its natatory setae embraced by the palps of the mouth-parts and the bases of the first trunk-limbs.

The broad, flattened basal article of the endopod (Fig. 3) articulates with the shaft on its inner surface near the apex. It bears two short setae which differ in structure in different species. The second article bears two setae of moderate, but unequal length, of which at least the apices are thin-walled. Besides these, in the male there are three very short setae, but not more than one of them is present in the female; in the female of *Conchoeia borealis antipoda* they are all absent. The end-article bears three 'tube-setae' similar to those of the antennule. In the male there is a clasping organ
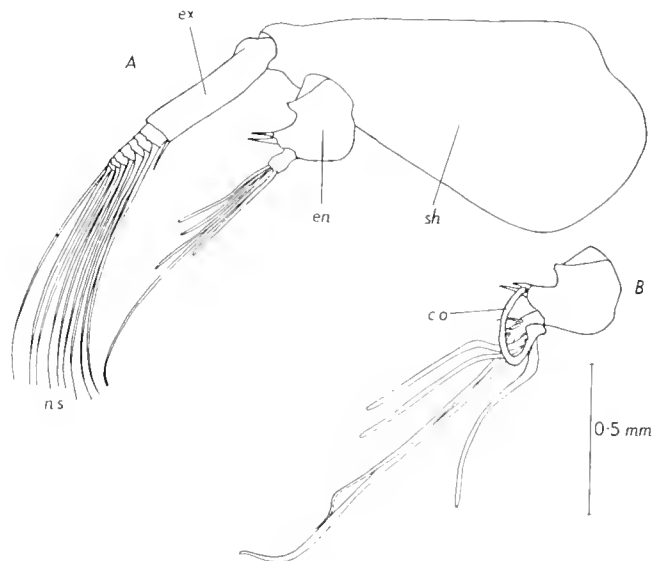

Fig. 3. *C. borealis antipoda*. Right antenna from inside. A, female; B, endopod of male.
c.o, clasping organ; *en*, endopod; *ex*, exopod; *n.s*, natatory setae; *sh*, shaft.

(Fig. 3 B, *c.o*) which Skogsberg (1920) considered to be a modification of the end-article itself. This is a hook-like structure which differs somewhat in form on the two sides of the animal, and also differs in different species. Normally the longer setae of the ramus extend vertically downwards, just within the anterior gape of the carapace; the ramus can, however, be moved antero-posteriorly.

The main adaptation of the antenna is for swimming. The exopod of the appendage can be extended through the antennal notch and moved freely, even when the valves of the carapace are tightly closed. The form of this notch and hollowing of the carapace below and behind it allow free backward movement of the exopod. The exact match in position of the articulation between the antennal exopod and shaft with the notch leads to the notch serving as a rowlock for the backward stroke of the oar-like exopod and its natatory setae. The articulation is bicondylar, with the one condyle ventral and the other dorsal but slightly displaced outward and forward. The main part of the musculature enclosed in the antennal shaft is the flexor musculature of the exopod. Skogsberg (1920) described the swimming action of the antennae and pointed out that it resulted in a forward propulsive stroke. In fact, the bicondylar articulation leads to the exopod swinging back in an arc with a slight downward movement. This downward movement gives a slight uplift to the front of the body exactly like that produced by our arm action in the breast stroke. Uplift in the water will also be produced by the boat-shape of

the carapace. In *Conchoecia borealis*, as in many other species, development of the shoulders of the carapace into sharp flanges provides hydroplanes which also contribute to uplift of the animal when it is swimming. The main component of the swimming-stroke can thus be concerned with forward propulsion.

As has been pointed out, the antennal endopod shows sexual dimorphism. The tube-setae are probably sensory, and in the male the hooked clasping-organ probably had a copulatory function.
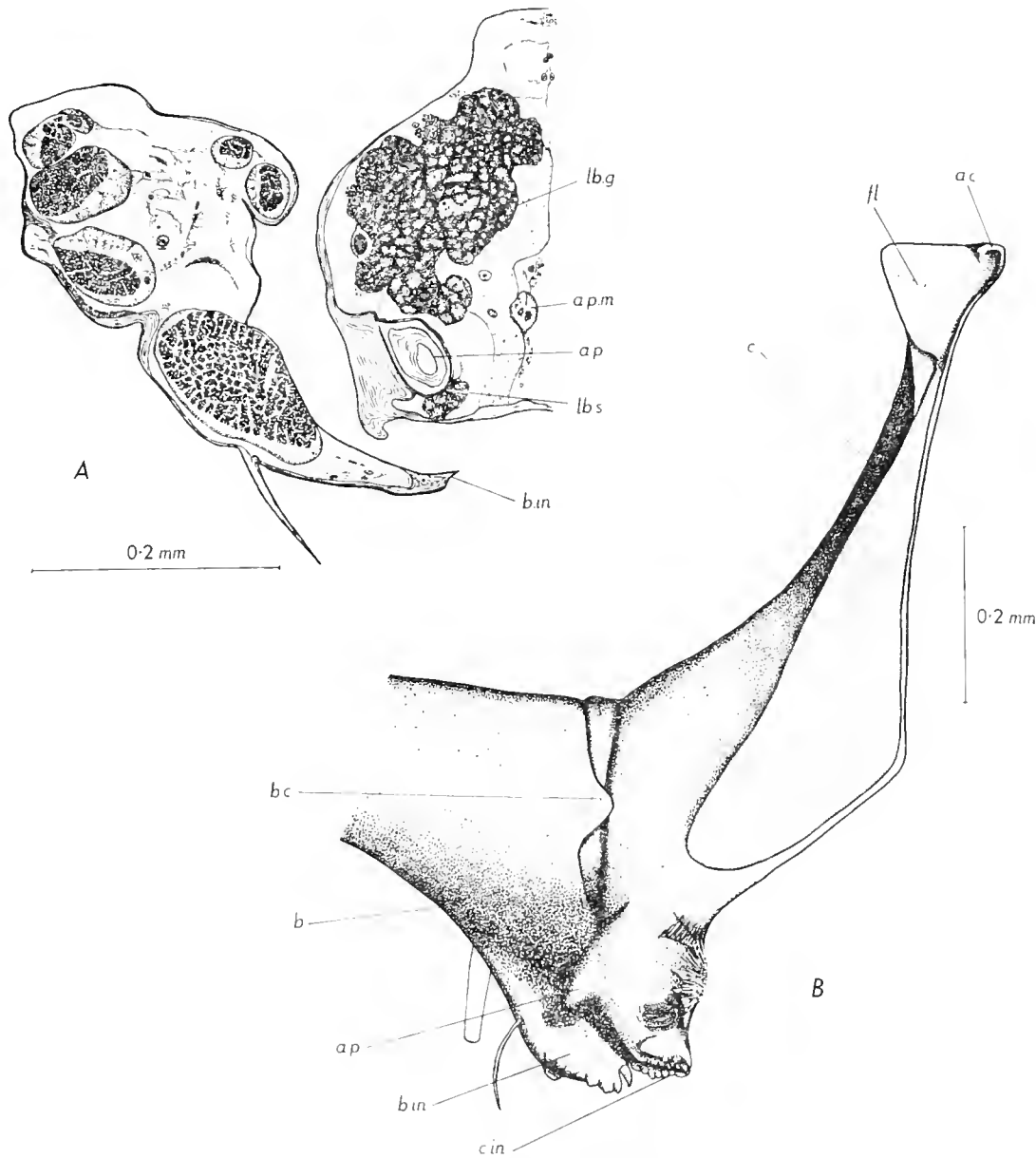
Fig. 4. *C. borealis antipoda*. A, transverse section through labrum and mandibular basis showing distal articular process of coxa in labral socket; B, right mandibular coxa and part of basis from inside. *a.c*, dorsal articular condyle of coxa; *a.p*, distal articular process of condyle; *a.p.m*, antero-posterior labral muscle; *b*, basis; *b.c*, articular surface of basis and coxa; *b.in*, incisor edge of basis; *c*, coxa; *c.in*, incisor edge of coxa; *fl*, anterior dorsal flange of coxa; *lb.g*, posterior labral gland; *lb.s*, wall of labral socket.

LABRUM (Figs. 2, 4, 7, 8, 10)

The labrum is well developed and filled with gland-cells. It is usually described as being helmet-shaped. In section, its ventral surface is flattened and its dorsal surface rounded (Fig. 4 A). It arises

ventrally in front of the mouth and projects forward below and between the shafts of the antennae. The vertical posterior surface forms an anterior boundary to the oral atrium (Fig. 8). The atrium is bounded laterally by the mandibles, paragnaths and maxillules, and leads antero-dorsally into the oesophagus, which is directed slightly forward and upward. The posterior wall of the labrum usually bulges back to some extent, between the mandibular coxae. It is, however, provided with antero-posterior muscles (Fig. 4 A, *a.p.m.*), which can draw it forward and so increase the volume of the atrium. It bears a median patch of short, fine, dorsally directed bristles (Fig. 8). Ventrally to the oral atrium, a thin flat surface, with thickened cuticle, extends back horizontally from the labrum like a shelf. This may be termed the labral lamina (Fig. 8, *lb.l*). Laterally, the posterior edge of this lamina takes the form of comb-like structures. The whole posterior surface of the labrum and the labral lamina is supported by sclerites continuous with the ventral sclerite system of the animal.

The labrum contains two systems of glands. The anterior of these consists of a number of large unicellular glands, closely packed and running dorso-ventrally. Their openings are evenly spaced over the ventral and lateral walls of the labrum. The openings can only be seen clearly in heavily stained material (e.g. with chlorazol black), when they appear as small crater-like depressions. The second system is a paired compound gland, the two components of which lie partly within the posterior part of the labrum (Fig. 4 A, *lb.g*), but extend into the body on either side of the oesophagus. These latter glands open through the posterior wall of the labrum into the oral atrium.
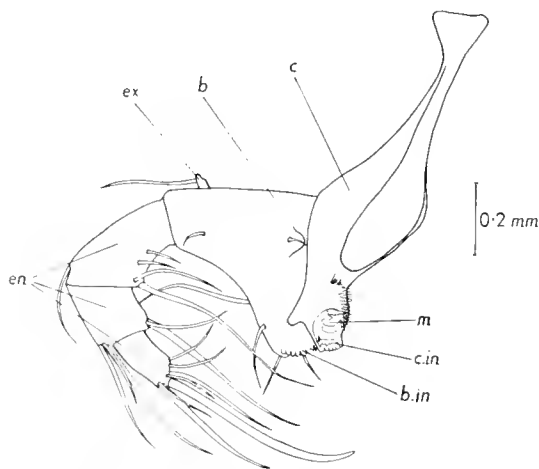

Fig. 5. *C. borealis antipoda.* Right mandible from inside. *b*, basis; *b.in*, incisor edge of basis; *c*, coxa; *c.in*, incisor edge of coxa; *en*, endopod; *ex*, exopod; *m*, molar surface of coxa.

MANDIBLES (Figs. 4, 5, 6)

Possibly the most interesting feature of the appendages of the Halocyprididae is the structure and articulation of the mandible. Each mandible is biramous, the endopod being large and pediform, the exopod minute. There have been frequent references in the literature to the presence of a gnathobase on its basis as well as on its coxa. This feature is in fact used as a character diagnosis of the whole group.

The *coxa* is elongate (Fig. 4 B, *c*, Fig. 5) and articulates with the side of the body immediately behind the base of the antenna (Fig. 2). The dorsal part is narrow and extends between the base of the antenna and the isthmus which links the carapace with the sides of the body of the animal. The anterior surface of this extension is laterally concave to accommodate the backward swelling of the antennal base. At the apex of the extension there is a cuticular thickening which forms the articular condyle (Fig. 4 B, *a.c*). Just beneath this condyle a rigid triangular flange (Fig. 4 B, *fl*) extends forward. Curving downward and inward below the articulation with the body, the gnathobase

(Fig. 4, *c.in*) extends into the oral atrium. As mentioned above, it forms a lateral boundary to the atrium (Figs. 7 and 8). Anteriorly at this lower end the coxa is produced into a distally directed process (Fig. 4 B, *a.p*), which Skogsberg (1920, p. 570) describes as more or less triangular and 'against which the endite on the following joint rests with an antero-inner edge'. Skogsberg also refers to the term 'Zahnhöcker' adopted by Claus (1891) for this process. In fact the structure is much more rounded than is suggested by these descriptions and is directed (it should be noted) much more nearly parallel to the longitudinal axis of the coxa than is shown in the figures given by Claus (1891, pl. XXII, figs. 6 and 15). The statement that the endite of the following joint rests on it is quite erroneous. No doubt Skogsberg based it upon observations of isolated mandibles. Examination of the appendage *in situ* and in section, shows that the process fits exactly into a thickened socket, which is part of the
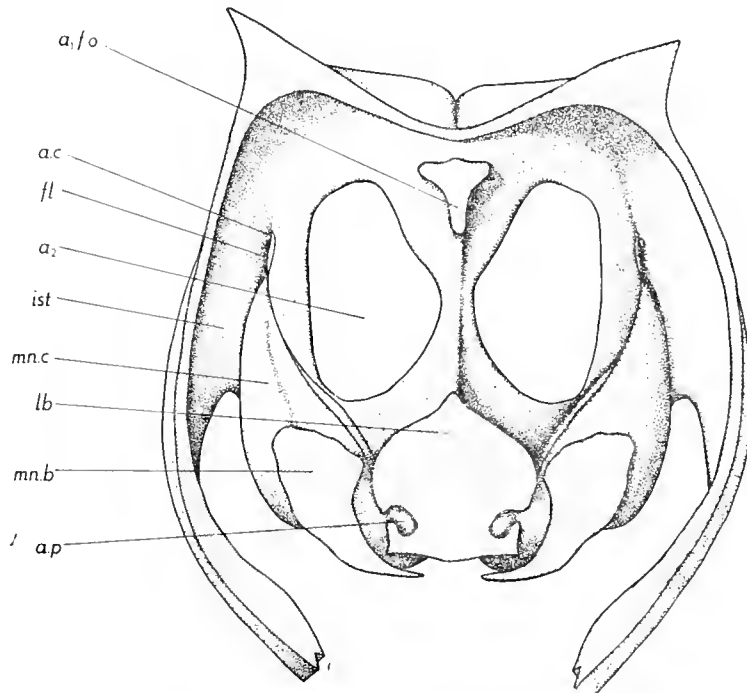

Fig. 6. *C. borealis antipoda.* Diagrammatic anterior view of a thick transverse section through mandibular region. (Antennal shafts omitted to show mandibular coxae.) $a_1 f.o$, base of antennules and frontal organ; a_2, antennal socket; *a.c*, dorsal articular condyle of mandibular coxa; *a.p*, distal articular process of mandibular coxa; *fl*, anterior dorsal flange of mandibular coxa; *ist*, isthmus linking body with carapace; *lb*, labrum; *mn.b*, mandibular basis; *mn.c*, mandibular coxa.

sclerite framework supporting the oral surface of the labrum (Fig. 4 A, *a.p* and *lb.s*, Fig. 8). The projection of this peg into the socket in the labrum is sufficiently deep to make it difficult to remove the appendage during dissection. The mandibular coxa is thus restricted in its movement to rotation about the axis formed by this articular process and the dorsal condyle. This axis, in fact, coincides fairly accurately with the anterior margin of the area of articulation of the coxa with the body (Fig. 4 B). In relation to the body of the animal, the axis of rotation of the coxa extends upwards, sloping slightly outwards and backwards (Figs. 2 and 6).

The mandibular musculature has been figured by Müller (1894, pl. 55). The extrinsic musculature of the coxa is in fact very much more complex than is shown in his figures. Full details of this musculature will not be given here, but it is significant that the arrangement of the muscular elements is such that they will rotate the coxae about the axes which result from their bicondylar suspensions. The anterior dorsal muscles originate near the hinge-line of the carapace and are inserted on the flanges anterior to the dorsal condyles. Since the axes of rotation of the coxae slope markedly out-

wards dorsally, these muscles extend at wide angles to them. Contraction of the muscles will result in outward rotation of the coxae so that their gnathobases separate. The posterior dorsal muscles originate near the anterior dorsals and are inserted on the posterior margins of the coxae. On contraction they will rotate the coxae inwards, bringing the gnathobases together. It is the transverse musculature which is so complex. Elements of it originate on various parts of the anterior hypostomal apodeme, or intermandibular tendons fused to it and on the antenno-labral apodeme. These are inserted on various parts of the coxae. The majority will rotate the coxae inwards, giving a powerful biting action by the gnathobases.

The coxal gnathobase is, as has frequently been pointed out, complex in structure. For the purpose of description it may be considered in four parts. Curving into the oral atrium distally, immediately above the posterior labral shelf, are three parallel incisor edges (Figs. 4, 5, Fig. 8, *c.in*). Although, as Claus (1891) pointed out, the structural pattern is more or less specifically constant, there is in *Conchoecia antipoda*, as in other species, some individual variation. Broadly speaking, the distal ridge, which extends the full width of the gnathobase, is, at least posteriorly, clearly divided into teeth. The middle and proximal ridges are much less regularly toothed, but always bear a long tusk-like posterior tooth. Dorsally to these ridges, the surface is shallowly concave. At the base of this depression there is a ridged pad, the masticatory pad (Fig. 5, Fig. 8, *m*). Skogsberg (1920) describes this as being covered with fine papillae placed close together. Müller (1894) more correctly refers to it as bearing isolated conical spines. These short sharp spines are so closely packed that the surface formed by their tips does in fact give the impression of being papillose. It is only by focusing through their depth in a whole mount, or seeing them in section that a true picture of the structure is obtained. The third region is the posterior margin of the gnathobase. Here there are four stout spines arranged in a dorso-ventral row (Fig. 8, *m.c*). These curve into the oral atrium and radiate slightly along the length of the row. Posterior to these teeth there is a dense group of radiating 'needle spines', each of about the same length as one of the teeth (Fig. 8, *m.f*). The fourth structure is a dorsal group of fine spines, almost continuous in distribution with the posterior group, but directed towards the mouth and projecting slightly into it.

The basis articulates with the coxa so that it extends forward almost at right angles to the latter (Fig. 4 A, Fig. 5). It is clear that its main movement is through a dorso-ventral arc, but rotation of the coxa about its axis will of course move the distal end of the basis laterally inward or outward. On the inner face of the basis, near its distal end, is a fine seta of moderate length, which extends inward across the labrum. At the anterior edge of the gnathobase are two setae, one long and one short, which extend ventrally. On the ventral surface of the gnathobase itself, are two further closely adjacent setae, which also extend ventrally and somewhat posteriorly. Near its distal end the basis bears dorsally a small mamilliform appendix (Fig. 5 *ex*, Fig. 7, *mn.e*), with a long anteriorly directed seta. Müller (1890, 1894) and Skogsberg (1920) have referred to this structure as representing the exopod of the appendage.

Proximally and ventrally a flange of the basis extends inward to form the gnathobase (Figs. 4, 5, *b.in*; Fig. 8). This gnathobase lies ventral and parallel to the incisor edges of the coxal gnathobase. It is separated from the latter by the backwardly projecting labral lamina (Fig. 8). The basal gnathobase consists of a single sharp biting edge formed by a row of six shouldered teeth. It is followed posteriorly by first an isolated spine, then a short, stout, spine-like seta. Ventral to the incisor edge is a single serrated tooth (Fig. 8, *v.t*). On the posterior ventral surface of the gnathobase are a series of short, stout, bristles. The basis and coxa articulate with each other by a fulcrum, which occurs about midway between the distal articular process of the coxa and the upper surface of the joint (Fig. 4 B, *b.c*). It is clear that rotation of the basis about this fulcrum will produce a backward and forward movement of

the gnathobase and this, if the coxa gnathobase remains rigid, will produce a shearing action. Rotation of the coxa will lead to a biting action of the gnathobases of the bases as well as of those of the coxae.

The two apical articles of the three-jointed palp are somewhat flattened transversely. The tip of the palp bears two stout claw-like setae (Fig. 5). These are pectinate on their posterior margins and curve posteriorly towards their tips. One of these claws is equal in length to the palp itself, the other is about two-thirds of this length. Besides these, there is, near by, a more slender seta of about the same length as the shorter claw and also a series of four fine setae of about half this length. A series of setae are present on the anterior margin of the palp. When the palp is folded inwards these extend towards the margin of the carapace. Distally on the middle article is a long stout pectinate seta, which is, however, more flexible than the terminal claws. Its length is such that it extends almost to the apex of the shorter terminal claw. Adjacent to it are two much shorter fine setae. A further short
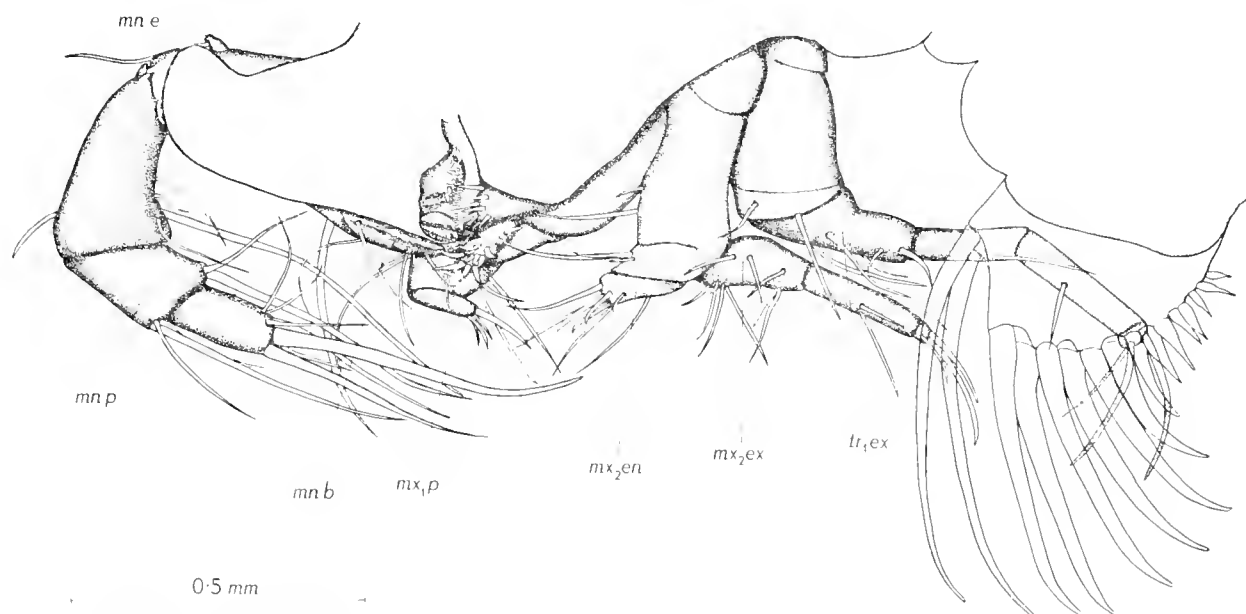

Fig. 7. *C. borealis antipoda*. Mouth and first trunk appendages viewed from mid-line; caudal furca in front of tips of trunk appendages shown in outline; armature of setae omitted. *mn.b*, mandibular basis (gnathobase); *mn.e*, mandibular exopod (mammiliform appendage); *mn.p*, mandibular palp (endopod); *mx₁ p*, palp of maxillule; *mx₂en*, maxillary endopod; *mx₂ex*, maxillary exopod; *tr₁ex*, exopod of first trunk limb.

seta arises near the apex of the proximal article. The posterior margin bears a further series of setae. There are two long pectinate setae of the same form as the long anterior one. The first of these arises near the distal end of the middle article and the other from a similar position on the proximal article. Both reach to near the apex of the shorter terminal claw. The middle article bears a shorter fine seta on its posterior distal margin and the proximal article three similar short fine setae distributed along the distal half of the posterior margin. All the finer setae bear fine secondary setules. The articulation of the proximal article of the palp with the basis is provided with lateral cuticular facets which limit its movement to a dorso-ventral direction. The limits of movement allowed by the articulation would seem to be from a position where the proximal article is directed nearly vertically upward from the basis to one with it directed vertically downward. The second and third articles can be extended straight in line with the proximal article or flexed toward the body. The articulation of the articles in series is such that the palp can be extended upwards and outwards, with the terminal claws near the antennal notch of the carapace, or folded downwards and inwards. Due to a slight diagonal setting of the articulation between the basale and the proximal article of the palp, the downward and inward movement is accompanied by a rotation of the palp about its axis, in such a fashion that the

short anterior marginal setae extend across the labrum towards the middle line (Fig. 10) and the short posterior marginal setae interlace with the ventral setae of the basale (Fig. 7). The length of the palp and that of the basis are such that during the downward arc of movement of the former, first the long posterior marginal setae, secondly the apical claws and lastly the long anterior marginal seta are drawn down the anterior margin of the carapace. At the posterior extreme of this movement, the terminal claws lie between the palps of the maxillulae and the endopodites of the maxillae. The posterior marginal setae lie with their tips pressed against the surface of the labrum. Finally the long anterior marginal seta lies just inside the ventral margin of the carapace, with its apex within range of the claws of the palp of the maxillule.

The outstanding structural features of the mandible are the presence of a gnathobase on the basis as well as on the coxa and the bicondylar articulation of the coxa. Skogsberg (1920, pp. 556–7) has pointed out that the mandible is used for holding food fast and for mastication. With reference to the incisor edge of the basis, he stated that as G. O. Sars (1887) pointed out, 'it seems to have the same function as the cutting part on the mandible of many other Crustacea, while the *pars incisiva* of the coxa serves as a sort of *tuberculum molare*, to break up the food more finely'. He stated that the latter process also serves partly as a 'cutting organ'. The bicondylar suspension of the coxa, which seems to be surprisingly uncommon in the Crustacea, is important in that it will enable an extremely powerful crushing action to be carried out by the gnathobases, while the firm proximal support provided to the palp will facilitate its independent movement. The disadvantage is that the arrangement will strictly limit the size of food-material which can be passed between the coxal gnathobases. Borradaile (1922) has described how in the shore crab (which also has a bicondylar suspension of the mandible) the food is first broken up by other appendages, before passing between the mandibles. In *Conchoecia*, it is difficult to see how, with the possible exception of the maxillules, appendages other than the mandibles could function in this manner. Quite clearly the shearing action of the gnathobases of the mandibular bases must have the function of cutting food into pieces which will pass between the gnathobases of the coxae into the oral atrium. This, as will be shown, is confirmed by the type of food material found in the stomachs of the animals.

The structure of the coxal gnathobase is complex and so also must be its function. It is interesting to note its division into incisor and molar processes in a manner similar to that of the mandibular gnathobase of the Malacostraca. There can be no doubt that the function of the incisor edges of these structures in *Conchoecia* will play an important role in breaking up food material passed between them. It is more difficult to visualize the function of the molar surfaces, with their closely packed spines. These probably would serve to grip and crush food-material, particularly if this were small, soft particles. The row of four teeth on the posterior margin of the molar surface must serve to retain food-material in the oral atrium, which same function in the case of smaller particles would be served by the fringe of fine spines. The fine orally directed spines will clearly aid transport of food-material into the mouth.

In his earlier work, Müller considered that the halocyprids might to a limited extent be bottom-living and use their mandibular palps for walking, as do the cypridinids. It is now clear, however, that they are planktonic during the whole of their life-cycle. This leaves the mandible free for its important role in feeding. The palp with its well-developed apical claws, extending beneath the oral atrium in the flexed position, and its wide arc of antero-posterior movement, is well adapted to grasping food and bringing it within the range of action of the mouth-parts. In dissected appendages it is difficult to see what function the marginal setae of the palp could possess in the whole animal, but when the palps are flexed it is evident that they could aid retention of food beneath the labrum and oral atrium.

PARAGNATHS (Fig. 8)

In the halocyprids the paragnaths are well developed. They extend ventrally immediately behind and closely investing the hinder margins of the mandibular coxae (Fig. 8, *p.g*). Each paragnath is triangular in shape and almost completely occupies the space between the mandibular coxa and the protopod of the maxillula. The anterior margin, where it borders on the mandibular coxa, is edged with a series of short fine bristles, which extend forward and inward towards the bristles on the margin of the molar surface of the mandible.

Functionally the paragnaths are important because they complete the lateral walls of the oral atrium. The anteriorly directed spinules of their anterior borders aid retention of food material within the atrium.
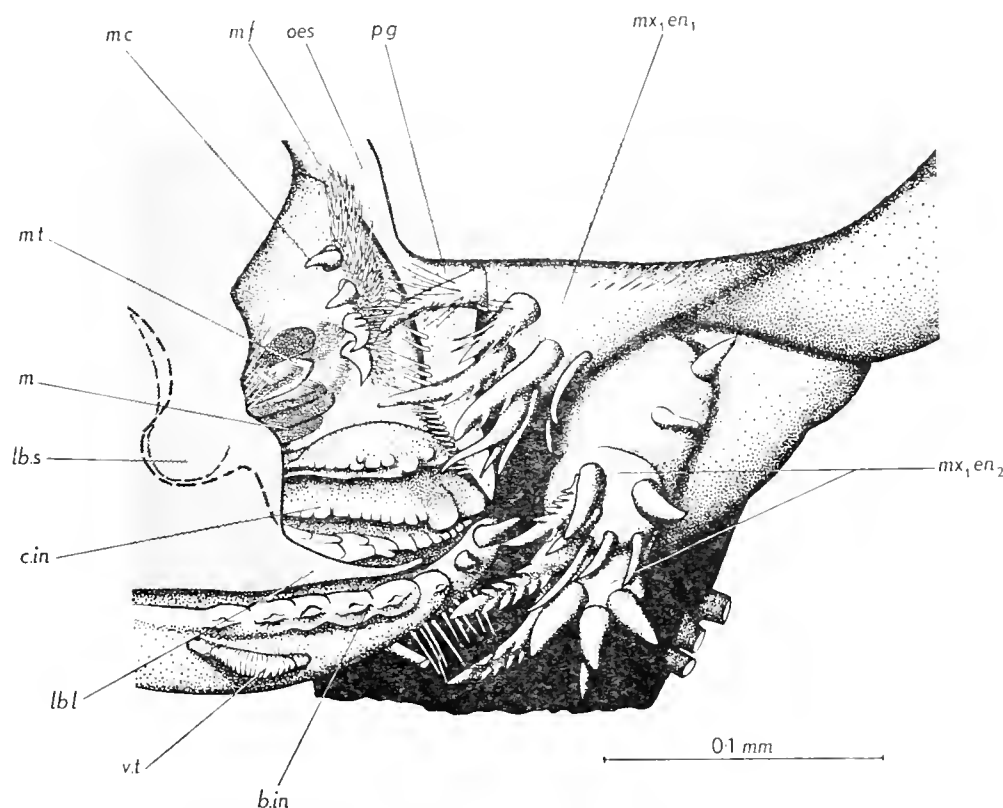

Fig. 8. *C. borealis antipoda.* View enlarged from Fig. 7 of oral atrium. *b.in*, incisor edge of mandibular basis; *c.in*, incisor edge of mandibular coxa; *lb.l*, labral lamina; *lb.s*, labral socket; *m*, molar pads of mandibular coxa; *m.c*, molar claws; *m.f*, bristle fringe of molar surface; *m.t*, molar tooth; mx_1en_1, pre-coxal endite of maxillule; mx_1en_2, coxal endites of maxillule; *oes*, oesophagus; *p.g*, paragnath; *v.t*, ventral tooth of basal gnathobase.

MAXILLULAE (Figs. 8, 9 & 10)

The maxillulae are uniramous, the endopod forming the palp and the protopod bearing well-developed endites. They arise ventro-laterally, immediately behind the paragnaths and project vertically downwards.

The proximal article of the protopod, generally considered to be the pre-coxa, is very short. The coxa is somewhat longer. There appear to be two endites (Fig. 8, mx_1en_1, mx_1en_2, Fig. 9), the proximal being pre-coxal, the distal arising from the coxa. The latter is, however, deeply bifid. It would seem useful to adopt the view of Müller (1894 *et seq.*) and Skogsberg (1920), who considered this endite to consist of two fused endites, comparable to the two distal endites of the cypridinids. The pre-coxal endite bears a series of stout setae, of which the two nearest the body are brush-setae, the more distal

anterior are pectinate and the remainder spine-setae. The proximal endite arises in the angle between the limb and the body. The ventral body-wall, in preserved material, usually bulges downwards between the proximal endites of the two sides, but is provided with muscles radiating to it from the anterior hypostomal apodeme. It would appear probable that this muscular system is used in conjunction with the labral muscle to enlarge the oral atrium. Depression of the body-wall must be by haemocoelic pressure, and flexure of the body. The middle and distal endites bear a series of powerful, inwardly directed spine-setae. The anterior spine-setae are pectinate with their secondary teeth apically directed. Skogsberg referred to the movable articulation between the articles of the protopod and their well-developed independent musculature. He also pointed out that the endites are not movable in relation to the articles from which they arise. Independent movement of the proximal
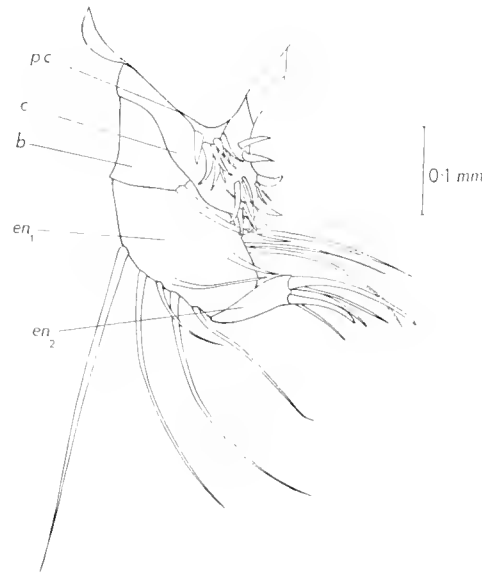

Fig. 9. *C. borealis antipoda*. Right maxillula from inside. *b*, basis; *c*, coxa; en_1, first article of endopod; en_2, second article of endopod; *p.c*, pre-coxa.

articles is great, but may be analyzed into two main components. One movement of each is rotation with respect to the length of the limb, thus swinging its endite through a horizontal arc. The other is a rocking movement which swings the endite through a small vertical arc. Skogsberg pointed out the marked divergence of the direction of the endites with the limb at rest. He did not, however, point out their range of movement or their relation to the other appendages. The proximal (pre-coxal) endites may be more or less directed towards one another across the body when its floor is raised. More usually they are directed forward between the paragnaths toward the incisor edges of the mandibular coxae; then the floor of the body is usually depressed. By an anterior rocking of the limb, their setae are thrust forward and upward between the molar spines of the mandibular coxae, their proximal brush-setae extending almost to the mouth. The coxa can move relative to the pre-coxa but the positions of its endites will also depend upon movements of the latter. The total range of movement of the coxal endites would seem to be from a position where they point straight across the body to one in which they point somewhat forwards and inwards between the mandibular gnathobases. They may be depressed to a position pointing slightly ventrally to the gnathobase of the mandibular basis or elevated so that they point towards the incisor surfaces of the coxa of this limb.

The palp of the maxillula (Fig. 2, Fig. 7 $mx_1 p$, Fig. 9) is generally accepted to be the endopod, but the basipod, which is very short and bears no endite is, as Hansen (1925) pointed out, partly fused with the first article of the endopod. The second article of the palp (first endopod article) is the longest of

the whole appendage. It is broad, being flattened laterally in relation to the animal. On its anterior border it bears a series of four long setae, which extend forward to the region of the outer setae of the basis of the mandible. On the posterior margin there are three long setae which extend ventrally and backwards outside the maxillary endites. The anterior edge and inner face bear three further setae, which extend medially beneath the endites, together with a single seta arising from the inner face of the basis. The terminal article is cylindrical, tapering only slightly towards its apex. In *Conchoecia antipoda* its length is only slightly greater than the width of the previous article and it is normally directed backwards at right angles to the axis of the palp. At its apex it bears a group of five setae. Two of these are stout claws, of which one is about two-thirds the length of the other. Two other setae are more slender, but claw-like, and of about the same length as the shorter main claw. The fifth seta is very slender and about the same length as the longest claw. All of these curve forwards. Müller (1894) stated that the endopod is so bent inwards that it lies nearly parallel to the endites of the stem. It is true that the palp may take up this position, but it may also slope outwards to some extent. Besides this, some antero-posterior movement can take place. The end-article seems only capable of movement through a dorso-ventral arc, relative to the preceding article. The extent of this movement is from a position in line with the rest of the limb to one pointing posteriorly almost at right angles to it. Rotation of the protopod about its axis results in movement of the apical article of the palp through a horizontal arc, so that its total field of action is fairly large. It can be extended backwards with its claws interlacing with those of the maxilla, or extended forwards with them lying over or between the gnathobases of the mandibular basis. It does not, however, seem that the claws can be extended into the oral atrium, or folded inwards sufficiently to reach the endites of the protopod of the limb.

It has been pointed out above, that the maxillulary palps have anteriorly curved apical claws and their movement must be mainly through a horizontal arc. In fact it seems probable that their main function must be to pass food material forward on to the gnathobases of the mandibular bases. The maxillulary endites are well developed, but their armature is very much less powerful than that found in the cypridinids where they are used for mastication of the food (Graham Cannon, 1933). It would seem that in halocyprids they have little masticatory function. The direction in which their few spines and setae point and their range of movement would indicate that the distal endites probably serve to grip food in the mid-line and to transfer it from the gnathobases of the mandibular bases to the region of the incisor edges of the mandibular coxae in the oral atrium. Similarly it seems likely that the proximal endites push food forward on to the molar surfaces of the mandibular coxae and aid transport of food into the mouth.

MAXILLAE (Figs. 7, 10 & 11)

The maxillae are biramous with one ramus jointed and pediform, the other unjointed. The protopod bears a well-developed epipod.

There has in the past been some variance of opinion regarding which pair of appendages the fifth pair of limbs of many ostracods represent. Graham Cannon (1925, 1926) has shown quite clearly that, on the basis of the segmental excretory organs, in *Cypridopsis vidua* (=*Pionocypris vidua*), they are the maxillae. There is no reason to doubt that they represent the same pair of appendages in the Halocyprididae. Besides this, however, there are almost as many opinions regarding the homologies of the parts of the limb as there have been workers on the group. This is too extensive a topic to consider here in detail. On the basis of the musculature and segmentation of the appendage, it would appear that Skogsberg's view (1920) is reasonable. This view is: that the shaft extending ventrally from the body of the animal (Figs. 7, 11) is the protopod; the inwardly directed distal 'endite' with
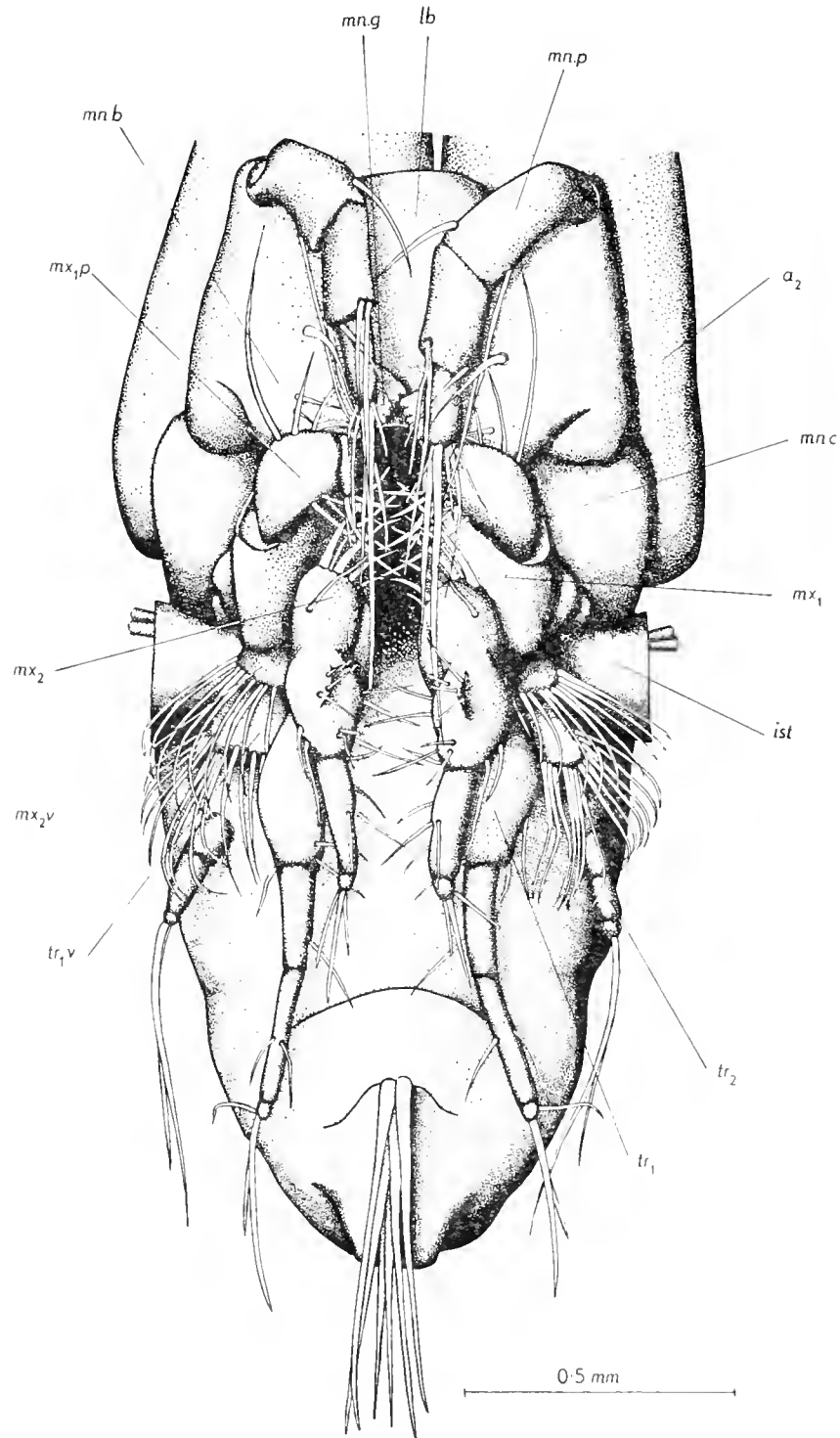
Fig. 10. *C. borealis antipoda.* Ventral view of body (only part of antennae included). a_2, antennal shaft; *ist*, isthmus linking body to carapace; *lb*, labrum; *mn.b*, mandibular basis; *mn.c*, mandibular coxa; *mn.g*, mandibular basal gnathobase; *mn.p*, mandibular palp; mx_1, maxillula; mx_1p, palp of maxillula; mx_2, maxilla; mx_2v, vibratory plate of maxilla; tr_1, first trunk limb; tr_1v, vibratory plate of first trunk limb; tr_2, second trunk limb.

independent musculature (Fig. 7 mx_2en, Fig. 11, *en*) is the endopod; and the long posteriorly directed pediform portion of the limb (Fig. 7 mx_2ex, Fig. 11, *ex*) is the exopod. The vibratory plate would then be an epipod. In general impression the limb is pediform. The protopod normally extends directly ventrally beneath the body from a ventro-lateral attachment, immediately in front of the isthmus,

which links the body of the animal with its carapace (Fig. 2, mx_2). In this position the vertical flattened epipod, in the form of a vibratory plate, extends outwards towards the carapace. Plumose setae, arranged in three groups, extend from the margin of this epipod. At the apex of the protopod is the large anteriorly directed endite-like structure, which, as already mentioned, is probably the endopod of the appendage. This bears at its apex a group of three pectinate claw-setae, which curve inwards and slightly backwards (Fig. 10). Dorsally and externally to them are three moderately long, anteriorly directed brush-setae. The setae of the endopod may be directed towards the apical claws of the maxillularly palp, but forward movement of the shaft of the maxilla brings them into the region of the distal endites of the maxillule. A degree of ventral extension of the endopod is also possible. Proximal to the endopod, there are on the shaft of the maxilla two groups of setae, borne on slight prominences, which probably represent endites. There are three setae in thedistal group, a long outer brush-seta, a median brush-seta of about half its length and an extremely short inner seta. The more
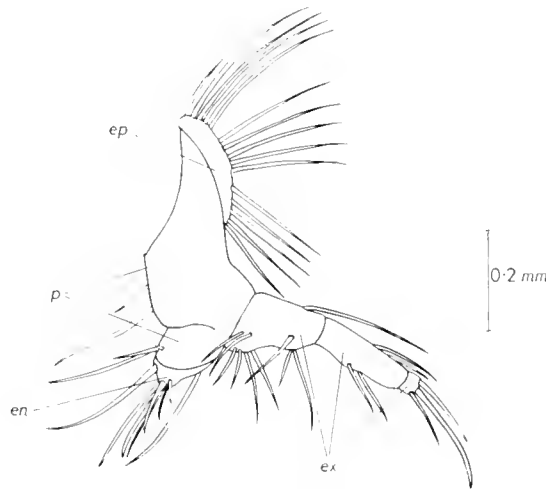

Fig. 11. *C. borealis antipoda.* Right maxilla from inside. *en*, endopod; *ep*, epipod; *ex*, exopod; *p*, protopod.

proximal group consists of a brush-seta of about the same length as the longest in the distal group and a much shorter seta. The setae in these two groups are directed towards the distal endites of the maxillule, though their position varies with movement of the shaft and they can be directed more dorsally towards the proximal maxillulary endites.

The exopod (Figs. 7, 10 and 11) is divided into three articles. The first two of these are long, the terminal very short. The articulation of this ramus is slightly to the outside of the distal extremity of the protopod and at rest extends back parallel to the body of the animal. At the apex of the exopod there are two long claw-setae which curve downwards, and a much more slender one. From the lower edge arise a series of setae extending downwards. These setae are in series with a long brush-seta extending downwards from the ventral surface of the endopod. Of them, there are four in a group arising from a prominence at about a third of the length of the proximal article from its base. A further pair arise near its apex. The second article bears a similar single seta about the middle of its length. A second series of setae arise from the median face of the exopod and extend inwards across the mid-line. There are on the first article two of these near to the proximal group of ventral setae and a third near the distal pair. The second article bears a single medially directed seta near its ventrally directed seta. Somewhat dorsally from the outer face arise a third series of setae, which extend backwards, upwards and slightly outwards. Two of these are near the apex of the proximal article and a third arises at about two-thirds of the length of the second article.

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Besides the antero-posterior movement of the shaft of the maxilla, the exopod is capable of similar movement. In preserved material it usually lies parallel to the margin of the shell, with its terminal claws directed straight back. It may, however, be flexed ventrally to produce a curvature of the limb, while the terminal article may be flexed so far that the claws are directed vertically downwards at right angles to the remainder of the limb. Professor A. C. Hardy has pointed out to me, in a personal communication, that the live animal quite normally extends the whole limb vertically downwards. Such a movement will draw the ventral setae and terminal claws forward along the ventral posterior margin of the carapace and bring the whole maxilla within reach of the inward arc of movement of the mandibular claws.
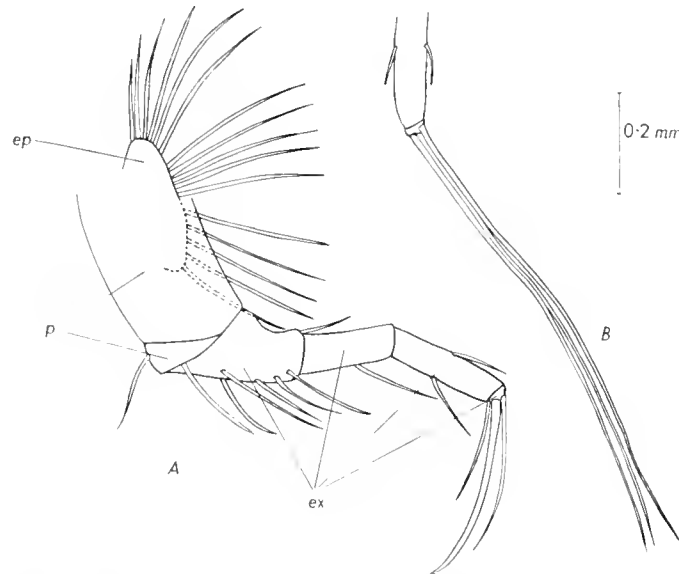

Fig. 12. *C. borealis antipoda.* A, female right first trunk limb from inside; B, apex of the same appendage in male. *ep*, epipod; *ex*, exopod; *p*, protopod.

With its wide range of antero-posterior movement and ventrally curved terminal claws, the elongate exopod of the maxillae may play some part in collection of food. The short endopods, with posteriorly curving claws, probably play a main role in food transport in conjunction with the maxillulary palps. The endites, as described above, are very poorly developed. Their long slender brush-setae may assist in forward transport of fine food-material, but can be of little use for manipulation of larger material. Marginal setae of the exopod may aid retention of food-material.

The epipod of this appendage, in conjunction with that of the first trunk-limb, undoubtedly creates a respiratory water-current through the carapace in a manner similar to that in *Cypridopsis* (= *Pionocypris vidua*) and in *Cypridina* described by Graham Cannon (1926, 1931). Müller (1894) had in fact observed this current in *Conchoecia* experimentally with the aid of carmine particles. He also described how the epipods beat continuously and independently of other movements of the limbs.

FIRST TRUNK-LIMBS

The first trunk-limbs are uniramous, jointed and pediform. The protopod bears a well-developed epipod. They show sexual dimorphism. Though very similar in general appearance to the maxillae, as pointed out by Skogsberg (1920), their endopods are even less well developed. The protopod of each arises immediately behind that of the maxilla so that it extends ventrally below the posterior extreme of the isthmus linking the body of the animal with the carapace. It bears an epipod similar to that of the maxilla. As might be expected from its position in relation to the protopod of the

maxilla, it bears no endites and no setae. The part of the limb which Skogsberg considered as the endopod bears a single long brush-seta extending forward towards the mid-line of the animal (Figs. 7 and 12). The exopod of the appendage (Figs. 7, 10 and 12) has four articles, the proximal being the longest, the distal, as in the case of the maxilla, being the shortest. In the female, there are two distal claws and a seta, similar to those of the maxilla, but in the male there are three extremely long natatory setae, which can curve upwards as far as the hinge-line of the carapace. Further setae on the exopod may be described as similar to those of the maxilla. Projecting ventrally there is a single apical seta on the inner face of the protopod in series with two further setae on the first article and one on the third article. Projecting towards the mid-line from the inner face are three setae on the first article, one on the second and one on the third. There is only one seta extending outwards from the limb, on the first article of the exopod. In addition, however, there are further setae (not represented) on the maxilla—a dorsal distal seta on the first article of the exopod and a dorsal medial seta on the third article.

Movement of the limb would seem to resolve into an antero-posterior movement of the protopod and a dorso-ventral extension and flexure of the exopod. The ventral flexure of the limb may not be as great as that of the maxilla but the dorsal extension is greater.

The epipods of these appendages beat in conjunction with those of the maxillae. It is possible that the limbs themselves could take part in collection of food, but the enormously elongate apical setae in the male are strongly suggestive of some function of locomotion in this sex.

Second trunk-limbs (Figs. 2 & 13)

The second trunk-limb (Fig. 2, tr_2, Fig. 13) is very short with three articles. It arises at the side of the body just behind the first trunk-limb. At rest it is directed dorsally and posteriorly. The only setae arising from this appendage are two apical setae, one of which is very long, extending to the posterior dorsal margin of the carapace and the second of which is only half the length. Müller (1894) described the movement of this appendage in some detail. Apparently, as its structure suggests, it is extremely mobile; it can be flexed or rotated freely.

The immediate function which comes to mind in the case of these limbs, with their position high on the side of the body of the animal and extreme mobility, is that of cleaning. Müller, however, pointed out that these limbs cannot reach the epipods of the maxillules and maxillae, the most obvious structures to require cleaning. Furthermore he described how these structures are self-cleaning. Müller was, in fact, not able to observe the second trunk-limb performing any definite function. Some doubt must thus remain about this.

0·2 mm

Fig. 13. *C. borealis antipoda.* Left second trunk limb from outside.

Furca (Figs. 2 & 7)

The furca of the Myodocopa is so well known as to need little more than brief mention. Each furcal plate bears eight claws, an anterior group of four large ones and a posterior of four smaller ones. All eight claws radiate outwards from the furca, the most anterior one, which arises from the anterior border of the furcal plate, pointing markedly anteriorly. The more posterior claws point slightly backwards. All the claws are bipectinate on their posterior margins. Antero-posterior flexure of the trunk of the animal and hence antero-posterior movement of the caudal furca, can be considerable. Thus the trunk may be stretched out straight posteriorly to extend the caudal furca through the
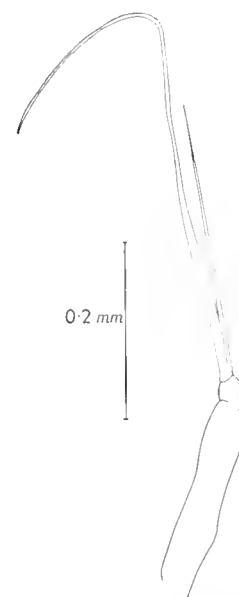
posterior gape of the carapace, or it may be flexed forward to bring the furcal claws between the bases of the appendages. In this latter position, the anterior claws extend between the endites of the maxillules, with their apices almost in the oral atrium. There can be no doubt that these claws have a cleaning function as is commonly the case in ostracods.

PENIS

The structure of the penis of the halocyprids has been described by Skogsberg, but though his and earlier descriptions make it difficult to understand the three-dimensional structure of the organ, this is not in itself relevant to the present topic. It is, however, worthy of note that this extremely large organ is unilateral and set well to the side of the animal. In this position, though it extends downwards to the ventral margin of the carapace, or even beyond, it does not impede the movement of the limbs and leaves a clear path for the flexure of the trunk and anterior extension of the caudal furca.

FEEDING-MECHANISM
TYPE OF FOOD

Müller (1894, 1927) stated that the stomachs of halocyprids contained the remains of copepods. He further stated that these have been trapped on the sticky shell, drawn in by the mandibular palps and conveyed with the sticky secretion of the shell-glands into the mouth and stomach. Elofson (1941) also found copepod remains in the stomachs of certain species of *Conchoecia* and I too have found such copepod remains in the stomachs of numerous species. I have even seen a specimen of *C. bispinosa*, which had a large part of the crushed but only slightly dismembered exoskeleton of a small copepod in its stomach; usually, however, the only identifiable remains are limbs, but it has not been previously noted that these are usually derived from animals of a size equal to or greater than that of the ostracod. It is difficult to understand how large prey could be trapped in a sticky secretion of the carapace, unless this secretion was much more copious than would be indicated by the size and number of the glands. In fact, the stout spines and claws present on the mandibles and maxillules, together with the powerful gnathobases of the former, give the impression of a voracious predator.

I have noticed that, whether or not there are any copepod remains in the stomach of a halocyprid, there is usually a mass of fine material. This confirms Müller's observations (1894); but in addition the material sometimes contains diatom remains, a fact not stated by Müller. The type of food contained in the stomach bears little relation to the size of the animal. Thus, some stomachs of the large *C. valdiviae* have been found to contain nothing but fine detritus while, on the other hand, those of the comparatively small *C. echinata* have had limbs and other remains of copepods obviously from animals larger than the ostracod. Diatoms and other fine detritus could have been derived from the copepods which had been eaten; frequently, however, as has been stated, such material may be present without any copepod-remains. Furthermore, the appendages, particularly the proximal endite of the maxillule, have, in addition to spines, an armature of slender setae and brush-setae, which is reminiscent of a particulate feeder (cf. *Cypridina antarctica* according to Graham Cannon, 1933).

FEEDING ON FINE MATERIAL

Whether diatoms or detritus are deliberately collected by *Conchoecia* as food or are swallowed accidentally is difficult to decide. There is no trace of any filter-feeding-structure in these animals, but there are two ways in which such material could be collected. Müller's description of the observations upon which he based his conclusions regarding the feeding of halocyprids provides evidence regarding one of these.

Müller described (1894, p. 109) how carmine particles, suspended in water in which *Conchoecia*

was swimming, became trapped in the sticky secretion of the marginal glands of the carapace. He observed this to be drawn in by the mandibular palps and formed into a mass by the mouth-parts. He pointed out that this process took place whether anything was trapped in the secretion or not. Elsewhere (p. 127) he stated that he was not able to observe directly that it was swallowed, but found that the stomach contents were similar in nature to this material. It is perfectly clear, from the structure of the mandibular palps, that they could draw in the secretion of the marginal glands from the front half of the carapace, as observed by Müller. The apical claws are suited to such function (Fig. 2), while the posterior marginal setae and possibly also the anterior marginal setae could contribute to the process. Müller (1894) held the view, repeated by Calman (1909), that the greater development of the anterior marginal glands of the carapace may be associated with this process. It is not, however, universally true that these glands are better developed than the others. In fact, if anything, *Conchoecia antipoda* has them less well developed. It would be possible, however, for the secretion from the more posterior parts of the ventral margin to be drawn forwards by the anterior curving claws of the maxillary exopod (Fig. 2). The possibility of the limb moving in this fashion has already been considered (page 316). The secretion could thus be brought within range of the movement of the claws of the mandibular palps and added to any food collected directly by them. The only appendages which can reach the posterior margin of the carapace, which is also provided with numerous glands, are the second trunk-limbs. Their fine setae are poorly adapted to movement of such material, while their range of movement could hardly bring it within reach of other appendages. Thus although food-material may be trapped by secretion from the glands of the carapace, these cannot be entirely subservient to this function.

The structure of the appendages shows that Müller's statement, that food-laden secretion dragged in by the mandibular palps is passed into the oral atrium by the palps of the maxillule, probably does not cover the whole process. It is improbable that the movement of these structures would be sufficient to pass material directly into the oral atrium. When the mandibles are folded under the body, their claws extend into the field of movement of the maxillary endopods (Fig. 7) which with their backwardly curved claws could easily withdraw material from the mandibular claws. The maxillulary palps, with their forwardly curved claws could then draw food-material forward from the maxillary endopods to bring it below the labrum in the region of the mandibular gnathobases.

The other possible method of collection of fine material is quite different. I have frequently noted that preserved material may have a mass of detritus held beneath the labrum by the open cage of setae formed by the infolded mandibular palps. This could of course have been passed forward by the maxillulary palps, and could also be contained in the secretion from the marginal glands of the carapace, which has been swept in by the posterior marginal setae of the mandibular palps. There is, however, another possible explanation for the presence of detritus in this region. The beat of the epipods of the maxillules and maxillae creates a water-current through the carapace, and will carry detritus with it. Müller (1894) has, indeed, described how detritus is carried in this manner in the live animal. A large part of the water-current must flow between the mandibular palps and over the surface of the labrum in just that region where the numerous openings of the anterior labral glands are situated. This resembles the food-collection mechanism described by Graham Cannon (1933) in *Cypridina*. There is no information available regarding the nature of the secretion of the labral glands in *Conchoecia* but, if it is comparable with that of other crustacea, it will be a sticky secretion which will entangle any detritus swept in with the water-current, as in the case of *Cypridina*. The secretion together with the detritus would then be held in place by the marginal setae of the mandibular palps and be available as a source of food-material. Whether detritus is collected in this manner beneath the labrum of *Conchoecia* as food-material can only be determined experimentally.

But by whatever means fine material is collected, it seems that it will be massed beneath the labrum, and that transport to the oral atrium must follow. It has been pointed out already that the downward arc of movement of the mandibular basis brings the incisor edge backwards and upwards into line with the distal endites of the maxillule. By this means the posterior spines and setae of the basal gnathobases, together with the gripping action of the incisor edges, could transport food-material into the path of forward-movement of these endites. By their shearing action, the basal gnathobases may at the same time cut up any larger material trapped in the secretion. During the upward arc of movement of the mandibular bases, the lateral combs of the labral lamina would retain material in the oral atrium.

Though the transversely directed spines of the distal maxillulary endites could play some part in trituration of food, it seems likely that this would mainly be with large material. It is possible that the peculiar structure of the molar pads on the mandibular coxae is an adaptation for trituration of fine material. Certainly such material, trapped in sticky secretion, would be retained between them by the fringing spinules on the posterior margin of the coxal gnathobase and on the anterior borders of the paragnaths. Forward thrusting of the proximal endites of the maxillules, with their brush-setae and pectinate spines (Fig. 7) together with that of the few long brush-setae of the maxillary endites, would all the time tend to move material forward and upward towards the mouth. Here the orally directed spinules of the coxal gnathobases of the mandibles, together with the spinules on the oral wall of the labrum, would finally bring food into the mouth. Peristaltic action of the oesophagus would then take over.

During the whole feeding-process, the marginal setae of the appendages must aid retention of material in positions where it can be manipulated by the appropriate appendages.

FEEDING ON LARGE MATERIAL

Despite his observations of live specimens, Müller quite clearly did not observe a *Conchoecia* feeding on a copepod. He found the copepod remains in the stomachs of specimens and related this to his observation of the way in which the animal collected the secretion of the marginal carapace glands with carmine particles trapped in it. He did not take into account the size of the prey. There is, then, no direct evidence that the secretion of the glands of the carapace is involved in capture of copepods. A powerful swimmer such as *Conchoecia* should easily capture a copepod, with the aid of its clawed mandibular palps. Whether the sticky secretion of the carapace glands, or perhaps the labrum, aid such capture by immobilizing the prey can be determined only by observation.

Copepod remains which are found in the stomachs of halocyprids are of such size that they would pass betweeen the bases of the trunk-limbs and mouth-parts. They usually show some evidence of crushing. From a specimen with an almost intact copepod in its stomach, it seems likely that captured prey swallowed without being broken up into smaller portions is crushed by the mouth-parts just sufficiently to enable digestion to take place. The initial grasping of such prey by the mandibular palps may possibly be aided by the maxillary exopods, the claws of which are apposed to those of the mandibular palp. It has been pointed out already (page 309) that, during inward flexure, the mandibular palps point slightly inward and rotate appreciably about their axes. Such movement would draw any prey inward and upward and press it firmly against the ventral surface of the labrum. The maxillulary palps could then help to grip the prey. A ventral movement of the apices of the mandibular bases will bring the shearing action of their gnathobases into play, but small prey would be moved back to pass between the bases of the appendages. In this position, manipulation of the food could be aided by the maxillulary palps and the maxillary endopods. Once the anterior end of the prey has

been moved back clear of the labrum, the maxillulary endites could, with their strong spines, grip it and probably to some extent crush it. A forward and upward thrusting of the endites would progressively move the prey through the oral atrium into the mouth. The angle at which the oesophagus leaves the oral atrium is of importance, in that there is no hindrance to direct passage of food into it. During transport of prey into the oral atrium, it would be subjected to further crushing by the coxal gnathobases of the mandibles, while the four posterior molar spines would aid transport by gripping the prey during the recovery movement of the maxillules.

It has been noted that the portions of larger copepods contained in the stomachs of *Conchoecia* are of such a size that they would just pass between the bases of the limbs and into the oral atrium, but the large specimens from which they are derived will not be able to pass. Each must be held below the level of the labrum mainly by the mandibular palps. The incisor edges of the mandibular bases could then shear portions, particularly limbs, from the prey. The slight rotation of the coxa, necessary to carry out this process, and the slight downward movement of the apices of the bases, would not prevent the palps from continuing to hold the prey in position. The secretion of the anterior labral glands could then entangle portions broken free and simplify their retention by the appendages. Further transport of these fragments probably resembles that of small whole prey.

THE APPENDAGES IN OTHER HALOCYPRIDIDAE

In order to add to the overall picture of the Halocyprididae it is of interest to compare the appendages of *Conchoecia* with those of other genera. A detailed comparison must, however, be postponed until more species of these other genera have been studied. Some characteristic features, however, may be considered. In *Euconchoecia* and *Archiconchoecia*, particularly, the setation of the antennule and the secondary sexual characters of the antennal endopod of the male differ from those of *Conchoecia* but, apart from differences of the mandibular gnathobases and the enormously elongated terminal setae of the male first trunk-limb of *Euconchoecia*, the remaining appendages are closely similar in structure and interrelation in all genera. Of particular note is the fact that the mandibular coxa has an articulation with the labrum similar to that described on page 307 in *Conchoecia*. Not only does this show a functional similarity in the mandible, but it also provides a new taxonomic character common to the genera.

Among the halocyprid genera, differences may be seen in the structure of the molar surface of the mandibular coxa. Skogsberg (1920, p. 740) questioned the homologies of the masticatory pad and the oval cavity on the coxa of *Euconchoecia*. In *Conchoecia*, the molar pad is in fact situated in a slight depression, though this is less marked than the depression in the coxa of *Euconchoecia*. The main differences between this latter genus and *Conchoecia* would appear to be as follows. In *Euchonchoecia* the small sharp conical bristles of the central and proximal parts of the molar pad are absent. On the posterior and oral surface of the molar surface of the coxa, there are up to twelve or thirteen molar claws instead of only four as in *Conchoecia*. The marginal bristles are much less dense and the orally directed group seems to be absent. These latter are functionally replaced by the more proximal marginal claws. Skogsberg further pointed out that the claws can be folded inwards into the oval depression. The functional significance of this is unknown, but may be some adaptation to the transport of food in the oral atrium. The structure of the molar surface differs less in *Archiconchoecia*. The molar spine (Müller's spine 'D') is absent, and the molar claws and bristles are less well developed. The structure of the molar surface in the genus *Halocypris* has been discussed by Skogsberg (1920). In *H. globosa* it is very similar to that of *Conchoecia*. *Halocypris brevirostris* differs particularly in the absence of marginal molar claws. The condition in other species of the genus has not been described.

Skogsberg (1920, p. 584) considered, like Müller, that Claus was not justified in placing *H. globosa* in the separate genus *Halocypria*, since the differences were of 'so slight a nature'. He had not then studied *H. globosa* and when later (1946) he redescribed this species he revised his views somewhat. He then considered that in many ways the species was intermediate between *H. brevirostris* and *Conchoecia*. A definite decision on this question must be deferred until other species of the genus have been redescribed, but in view of the small variation in the structure of the coxal gnathobase in *Conchoecia* and the differences in other genera, it seems likely that Claus was justified in his opinion. The two species should probably be placed in at least separate sub-genera, if not separate genera.

Müller (1906) described the interesting species *Thaumatocypris echinata*. In many ways this resembles the halocyprid genera; in particular the mandible possesses a gnathobase on the basis as well as on the coxa. The maxilla and first trunk-limb are similar to those of the halocyprids and bear similar vibratory plates. Though its distal article differs from, the maxillule somewhat resembles, that of *Conchoecia*; there are, however, many differences, the most remarkable of which would appear to be the absence of an antennal notch. This would seem to be related to the fact that though the antennal shaft and exopod are similar to those of the halocyprids, the endopod also is well developed and has a natatory function. In addition the antennule is distinctly segmented and is possibly natatory (Skogsberg, 1920, p. 119). In relation to these differences Skogsberg discussed the stabilizing effect of the spines on the carapace. It is also noteworthy that the caudal furca differs from that of the halocyprids. It would be interesting to know if the mandible has a similar articulation to that of the other halocyprids. Müller's figures (1906, pl. VI) indicate that there are many differences in the incisor edges of the mandible, while the molar surface must be of quite different structure. In addition the terminal setae of the mandibular palp are elongate and not claw-like. The figures and description give no reference to any process on the coxa, which could represent the articular process of other halocyprids. If such an articulation is absent, it would add further weight to the differences between the *Thaumatocypris* and the other halocyprids. The impression is that Müller was justified in placing his species in a sub-family separate from that including the other Halocyprididae.

COMPARISON OF HALOCYPRIDIDAE AND CYPRIDINIDAE

Skogsberg (1920) compared the morphological details of the appendages of the Halocyprididae with those of the Cypridinidae, but did not compare the whole animals from a functional viewpoint. Graham Cannon (1931, 1933) has made such a comparison between the Cypridinidae and the Podocopa. A similar comparison with the Halocyprididae is of interest.

An immediately obvious difference between *Conchoecia* and a cypridinid is the form of the carapace and the antennal notch (Fig. 14). In the former group, the carapace is usually elongate with a straight hinge-line and is very light and delicate; in the latter it is generally rounded with a curved hinge-line and is heavily calcified. The antennal notch of *Conchoecia* extends back very nearly parallel to the hinge-line with a well-developed rostrum above. Behind the notch, the surface of the carapace is hollowed to allow free backward swing of the antennal exopod. In the Cypridinidae the antennal notch is narrower and usually slopes upward towards the hinge-line; there is no prominent rostrum. Associated with differences in the carapace there is a difference in posture of the animal. In a typical cypridinid the main axis of the body slopes anteriorly upward much more markedly than it does in *Conchoecia*. The ventral apodemes, which are similar in the two groups, indicate an upward curvature of this axis much further forward in *Conchoecia* than in *Cypridina*. The nervous system, also, extends further to the posterior in *Conchoecia* (cf. Claus, 1891, pl. 1, fig. 11 and Graham Cannon, 1931, fig. 10 B). The antennal shaft adds to the appearance of anterior uptilting in *Cypridina*.

In many members of this genus it is as broad as it is long and its longitudinal axis slopes upward. In *Conchoecia* it is elongate and extends forward. The orientation of the body of *Conchoecia* is similar to that of the Podocopa and it is possible that this is more primitive. It is, however, suggested that the orientation of the body and arrangement of the antenna and antennal notch is partly adapted to differences in the mode of swimming in the two groups. As has been mentioned when considering
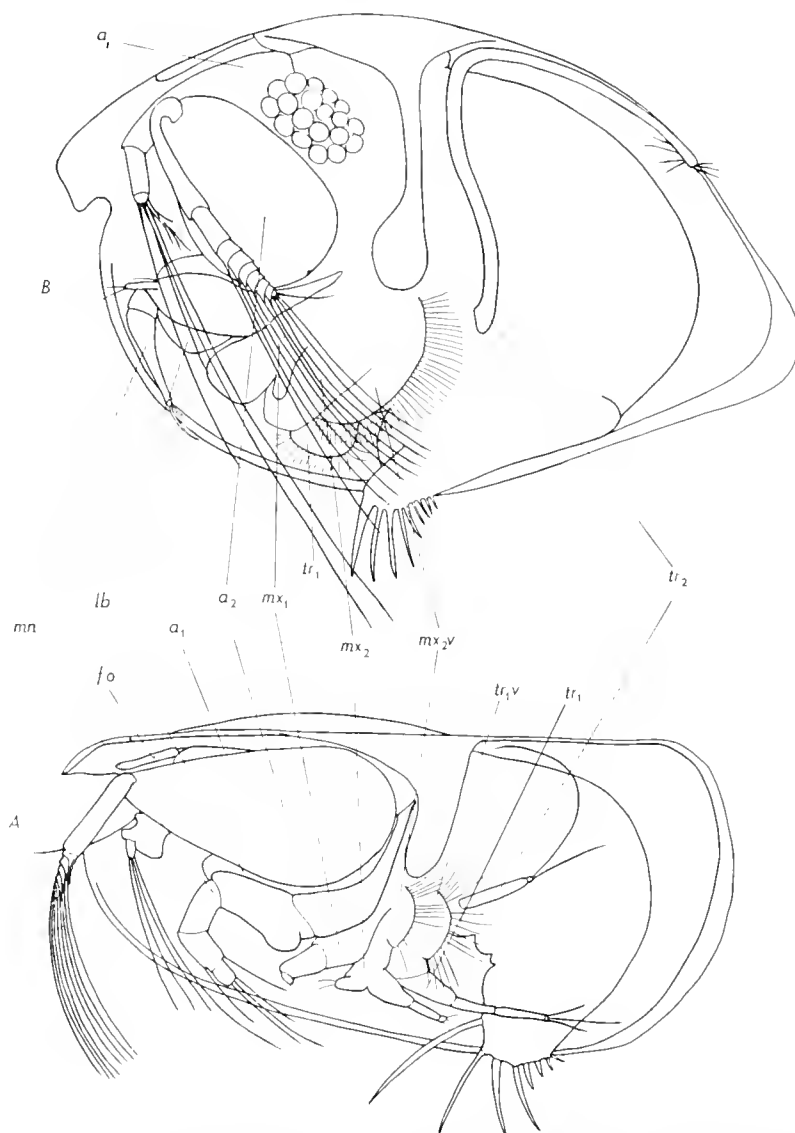
Fig. 14. Diagrams comparing A, *C. borealis antipoda*, and B, *Cypridina* (*Macrocypridina*) *castanea*. a_1, antennule; a_2, antenna; *f.o*, frontal organ; *lb*, labrum; *mn*, mandible; mx_1, maxillule; mx_2, maxilla; mx_2v, vibratory plate of maxilla; tr_1, first trunk limb; tr_1v, vibratory plate of first trunk limb; tr_2, second trunk limb.

the function of the antenna, the swimming action in *Conchoecia* is a forward propulsive stroke with only a small downward component, associated with the light, boat-shaped carapace. In the Cypridinidae, though there is a forward propulsive stroke (as mentioned by Skogsberg (1920)) the greater downward component is associated with the heavy, often rounded carapace. Even in those Cypridinidae such as *Cyclindroleberis* which have an elongate carapace, the body and antennal shaft have a marked upward slope anteriorly. It is interesting that in the genus *Halocypris* where the carapace is heavy and rounded rather like that of a typical cypridinid, the orientation of the body and antennal shaft also is more like that of a cypridinid; and the antennal notch is also more shallow.

The other interesting comparison is the adaptation of the appendages for feeding. Graham Cannon

1931, 1933) has pointed out that in the Cypridinidae there has been a backward shift in adaptation of the limbs for this purpose. Here, instead of the mandibles, the maxillules and maxillae are the main biting-mouth-parts. This is accompanied by a more posterior position of the mouth relative to the appendages. Thus the mouth lies posteriorly to the mandibular coxae, the oral atrium being bounded laterally by the maxillulae; the paragnaths are not developed. In *Conchoecia*, however, like the Podocopa, the mandibles are the main biting-mouth-parts, with the maxillulae playing only a small part in the process and the maxillae not adapted at all for biting the food. In this genus the mouth lies between the mandibular coxae, which also laterally bound the oral atrium, and the paragnaths are well developed. The difference in adaptation of the appendages for feeding is correlated with adaptation for walking. Thus in bottom-living cypridinids the mandibular palp is used for walking and the mandible is no longer used for biting the food. The gnathobase is reduced and adapted merely to assist transport of food into the mouth. The same pattern is retained in planktonic members of the group, such as *Gigantocypris* (see Graham Cannon, 1940), or *Cypridina (Macrocypridina) castanea* (see Graham Cannon, 1933) which is illustrated for comparison with *Conchoecia* in my Fig. 14. In the Podocopa, on the other hand, it is the antennal endopod which is used for walking and this leaves the mandible free for biting the food. *Conchoecia* does not walk at all and the mandible is free for biting the food. The palp, though well developed, differs in structure from that of the Cypridinidae and is used for capture of food.

SUMMARY

The functional interrelation of the appendages and their setae in *Conchoecia borealis antipoda* is described. Apart from differences in secondary sexual characters, there is little difference in other members of the genus *Conchoecia*.

A new feature of the articulation of the mandible with the body has been found in the Halocyprididae. A distally directed condyle on the distal apex of the coxa articulates in a skeletal socket on the oral surface of the labrum. This with the usual dorsal condyle restricts movement of the coxa to rocking about a vertical axis.

The anterior dorsal extrinsic muscle of the mandibular coxa is inserted on a flange which extends forward from the region of the dorsal condyle. This muscle thus serves to rotate the coxae outward and separate the mandibular gnathobases.

It has been confirmed that members of the genus *Conchoecia* are mainly predators on copepods. The method of capture and mastication of such food is discussed. The gnathobase of the basis of the mandible is probably concerned with reducing such food to a size that can be swallowed.

It seems probable that *Conchoecia* species can also feed on fine material. This may be collected by the secretion of the marginal glands of the carapace or by labral gland secretion.

The appendages of *Archiconchoecia*, *Euconchoecia* and *Halocypris* are in general similar in structure and arrangement to those of *Conchoecia*. Their mandibles have the same type of articulation. There are, however, differences in the gnathobases of the mandibular coxae, which must result in functional differences needing investigation.

The differences in the gnathobases of the mandibular coxae of *Halocypris globosa* and *H. brevirostris* are probably of sufficient significance to warrant inclusion of these species in separate genera, as suggested by Claus.

A redescription of *Thaumatocypris echinata* Müller is necessary, in order to clarify its systematic position.

Conchoecia is compared with *Cypridina*. The functional pattern of the mandibles and more posterior limbs of the former, as well as the position of the mouth, do not show the backward shift present in Cypridinidae.

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REPRODUCTION, GROWTH AND AGE OF
SOUTHERN FIN WHALES

By

R. M. LAWS

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REPRODUCTION, GROWTH AND AGE
OF SOUTHERN FIN WHALES

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(Plates IV–VII and Text-figs. 1–60)

GENERAL CONSIDERATIONS

INTRODUCTION

IN his paper on the southern stocks of whalebone whales, Mackintosh (1942) summarized the work which had then been published and discussed some additional unpublished data. He remarked that 'In recent years a good deal of new material relating to the breeding, growth, and age of whales has been collected by members of the Discovery Committee's staff and other biologists who have sailed in factory ships to the Antarctic. Work on this material, which includes records of large numbers of ovaries, has been interrupted by the war, but it is hoped that it will be resumed in the future and much progress should be revealed when the results are available' (p. 216); and later (p. 226), 'The most important problem is to ascertain how many corpora lutea on the average are added each year in a sexually mature female'. Annual collections of ovaries were initiated, and have been continued, as a means of comparing the relative condition of the stocks of whales from year to year. A great deal of extra material has, therefore, accumulated since 1942 and continues to increase yearly. In a series of papers (Mackintosh and Wheeler, 1929; Wheeler, 1930; Wheeler, 1934; Peters, 1939; Mackintosh, 1942) attention was drawn to the use of counts of the corpora lutea and corpora albicantia in fin-whale ovaries as a measure of age. Ovarian scars have also been used for determining age in other groups of animals, for instance seals (Bertram, 1940; McLaren, 1958; Mansfield, 1958), the cow (Dawson, 1958), birds (Maynard, 1888; Wynne-Edwards, 1939), and even insects (Bertram and Samarawic-krema, 1958). Several estimates of the annual rate of accumulation of corpora albicantia in fin whales have been published ranging from 0·9 (Peters, 1939) to 2·5 (Wheeler, 1934), but they do not stand up to detailed criticism. When the present investigation began the main objects were to establish to what extent corpora albicantia persist in the fin-whale ovaries, and to determine the average annual increment of corpora and the range of variation, so that they might be used to estimate the age of whales. There are also many reasons why a better knowledge is needed of the whole breeding cycle of fin whales and other species. It is of intrinsic biological interest and it has an important bearing on population dynamics and on practical problems arising from the regulation of whaling.

Two main approaches to the solution of these problems have been made. One is by way of a detailed study of the gross and microscopic anatomy of the ovaries. The other is by investigation of the annual reproductive cycle of the species. These are dealt with in the two main parts of this paper.

My own interest in this work began when I spent the antarctic whaling season 1953/54 on board the floating factory 'Balaena', and the time has come to present the results of this recent work although new material continues to arrive. One considerable disadvantage is that it has still not been possible to study the breeding biology of fin whales directly, in the breeding areas. In fact we still do not know with certainty the location of these areas, though we may confidently assume that they lie in the tropical and subtropical zones of the oceans. Even if the breeding herds were located it is

hard to see how the anatomical and physiological work which is really needed could be done in such regions except at prohibitive cost. Such work is only made possible in the Antarctic by taking advantage of the facilities provided by the existing whaling operations.

With the exception of a few observations made at South African whaling stations (Saldanha Bay 33° 1' S., 18° 0' E., and Durban 29° 52' S., 31° 1' E.) some 30 years ago all the material on which this work is based has been collected during a few months of the year in the Antarctic, where the animals migrate to feed on krill. Since the 1950/51 season the pelagic whaling operations for fin whales in the Antarctic have been confined to January, February, and the first part of March. As the main part of the pairing season is from May to July, elucidation of events at this, the most important stage in the annual cycle, could hardly be more difficult. Even the observations from South African land stations are not truly representative of the breeding population, because they are situated near migration routes at positions probably well south of the breeding grounds.

It is therefore necessary to make inferences from the condition of animals killed in the Antarctic as to the events in the breeding season some six months previously; a procedure which is only justified by necessity. One species of baleen whale, the humpback whale, *Megaptera novaeangliae* (Borowski) has recently been studied on or near the breeding grounds (which in this species are in inshore waters) and is described in a series of important papers by Chittleborough (1955 *a*, 1955 *b*, 1958). We may, with certain reservations, draw on this work for comparison.

Part of the original work described in the present paper has already been presented in two short preliminary papers (Laws, 1958 *a*, 1959 *b*).

kindly made his preliminary analysis of the accumulated data on the ossification of the vertebral epiphyses available to me. I am also indebted to Professor J. T. Ruud and Mr Åge Jonsgård for interpreting some baleen-plate material.

Mr A. Style has drawn most of the figures in this paper and Mr A. Madgwick is responsible for some of the photographs.

In the preparation of this paper I have greatly benefited from discussions with Mr S. G. Brown, Dr R. G. Chittleborough and Mr Å. Jonsgård. I should also like to thank Dr Mackintosh and Dr Bargmann for their help at all stages of the work.

MATERIAL

Investigations of the breeding biology of whales have to be based on systematic examination of the reproductive organs, and the following routine observations and collections are made when possible by biologists working in floating factories.

Both sexes

1. Date, noon position of factory.
2. Length of whale measured in straight line from tip of upper jaw to notch of tail.
3. Physical maturity; condition of vertebral epiphyses (Wheeler, 1930).
4. Baleen plate for examination (Ruud, 1945).
5. Measurement of blubber thickness.
6. Observations on diatom film (Hart, 1935), parasites, scars, etc. (Mackintosh and Wheeler, 1929).
7. Since 1955/56 ear-plugs have also been collected (Purves, 1955; Laws and Purves, 1956).

Females

8. Sexual maturity.
9. Foetus present or absent (uterus searched, or not ascertained). If present sex and length and if possible weight are recorded.
10. Condition of mammary gland; greatest depth and whether virgin, resting, intermediate, or lactating (Mackintosh and Wheeler, 1929).
11. Collection of ovaries, mainly from mature females (fixed and stored in 10% formalin).

Males

12. Measurement of testes and collection of specimen.

By far the most useful information comes from the ear-plugs and ovaries. In the antarctic pelagic whaling season 1953/54, in addition to the usual routine observations, I made a detailed study of a series of 168 pairs of fin-whale ovaries collected at relatively short post-mortem times (1–14 hr.). The main purpose of this study was an investigation of the variations in the morphology and histology of the corpus luteum and corpora albicantia. Specimens were fixed in formalin, Bouin, Heidenhain's Susa, Zenker-formol and Zenker-formol with post-osmication. One important practical conclusion was that for standard routine examination of whale ovaries some uniform method of slicing was essential and in 1954 a commercial bacon-slicing machine was acquired. With this machine slices of uniform thickness down to 1 mm. can be produced if the material has previously been hardened either by freezing or by storing in formalin. In routine examination 5 mm. slices are cut and all ovary material obtained since 1954 has been treated in this way.

Between 1934 and 1939 and again from 1945 to 1955 through the kind co-operation of a number of whaling companies annual collections of blue whale (*Balaenoptera musculus*) ovaries were received and examined. With the decline in the catch of blue whales these collections were decreasing in importance and in the season 1955/56 the whaling companies were asked to collect fin-whale ovaries. The companies' collections for this season totalled 334 pairs of fin-whale ovaries. Date, and position,

length, and size of foetus if present were recorded. In 1954/55 and 1955/56 a further 159 pairs of ovaries were collected by whaling inspectors and biologists in the three British floating factories and numerous other observations were made. The methods of examining this material have been standardized and it has provided much of the data for this paper.

In addition to this recent material I have had access to the records kept by the 'Discovery' Investigations from 1925 onwards (since 1949 incorporated in the National Institute of Oceanography). The data which are of relevance here consist mainly of observations of length, physical and sexual condition, state of fusion of the vertebral epiphyses, counts of the number of corpora lutea and albicantia, some measurements of the dimensions of these bodies, and measurements of the genitalia and foetuses. There are in addition limited collections of ovarian and testis material. The most important part of this varied material is in the form of counts of the ovarian corpora made by no less than fifteen different observers. One consequence of this is that there is a considerable variation in the quality of the work, since the different workers have applied different methods and criteria. It is difficult to make allowance for these variations and although all the records have been freely used in the course of the work it is preferable, where possible, to rely mainly on the more recent material to illustrate the present paper. For this reason there are discrepancies in amount of material between the various tables in this paper, but it is scarcely practicable or necessary to explain these discrepancies in every case.

PREVIOUS WORK

The first comprehensive studies of southern hemisphere fin whales were undertaken by the 'Discovery' Investigations in 1925, although Barrett-Hamilton (Hinton, 1925) had examined some 300 whales at South Georgia in 1913/14. This early work and later research by various workers up to 1940 is reviewed by Mackintosh (1942). The anatomy of the urino-genital system of fin whales has been described by Ommanney (1932) who dissected four foetuses.

Mackintosh and Wheeler (1929) worked at South Georgia and Saldanha Bay and their paper based on 1577 fin and blue whales established the general outline of the biology of these species and remains the most important single source of information on the biology of the fin whale. Consideration of the time of follicular ripening; the occurrence of corpora lutea of ovulation, and minute foetuses; the onset of increased testis activity in males, all suggested the earlier part of the southern winter as the beginning of the breeding season. These workers plotted foetal lengths, drew a mean growth curve, and by assuming all foetuses grow at the same speed they calculated the proportions conceived in different months. The majority of pairings appeared to take place in June and July and the gestation period was estimated to be just under a year. From the sizes of the largest foetuses and smallest calves they concluded that the average neonatal length of fin whales is 6·5 m. The length of the calf at weaning was estimated in a similar fashion to be about 12 m. and the lactation period to last about 6 months on average, from mid-June to early December. From these conclusions and because approximately half of the adult females they examined were pregnant they decided that each breeding cycle usually lasted 2 years. However, Wheeler (1930) was aware that in the fin whale a post-partum ovulation can result in one pregnancy being followed immediately by a second. From an examination of length frequencies they concluded that it was likely that both blue and fin whales attained sexual maturity at an average age of 2 years, and they gave figures for the average body length at sexual maturity for both sexes.

They showed that in general the number of corpora lutea and corpora albicantia in the ovaries increased with increasing body length, which suggested that corpora albicantia persist and accumulate in the ovaries during life. Ovulation was shown to be spontaneous, and they advanced arguments for

believing the females to have a polyoestrous cycle. The abundance of ripening graafian follicles is suggestive; the protracted breeding season allows time for several dioestrous cycles; and the fact that some whales, with more than 30 corpora albicantia, must be more than 30 years old if monoestrous was thought to be important.

If the female is polyoestrous and individual females become pregnant at 2-yearly intervals, then up to, say, six ovulations may be possible in one season. Because female whales are gregarious it could be expected that their experience would be similar and each year a certain number of ovulations would tend to occur more commonly than others. When they plotted the frequencies of corpora in their material they found peaks occurring at 4–5, 12, and 19 corpora and suggested that these represented the increase in numbers of corpora at intervals of 2 years. Wheeler (1930) developed and modified this hypothesis. He examined the state of fusion to the centra of the vertebral epiphyses and by this criterion classed individuals as physically mature or immature. With less than 15 corpora females were almost invariably physically immature, and with more than this number, physically mature. The frequency distribution of corpora in his larger material shows maxima at 1, 7, 11, 18 and 21 corpora. Three of these peaks precede physical maturity. He pointed out that in the first group the greatest number of corpora is at the beginning, which meant that the first ovulation was usually followed by pregnancy, whereas in subsequent seasons unsuccessful ovulations were thought to precede pregnancy. The importance of this work lies in the fact that it established a close relation between the attainment of physical maturity and the rate of accumulation of corpora. The fact that there is so little variation in the number of corpora accumulated at physical maturity implies that the rate of accumulation is very regular and/or very small. Wheeler's work suggested that there were on average three breeding seasons before the attainment of physical maturity so that about five ovulations occur each breeding cycle, or on average 2·5 per year.

In a later paper Wheeler (1934) applied this method of age-determination to 472 mature females for which records were available and calculated average mortality rates. We know now that the peaks in the frequency distribution of corpora in his material are not significant, but his figures demonstrate that the decline in numbers of fin whales of increasing ages (as shown by corpora numbers) in his sample, is exponential. Brinkmann (1948) published the results of investigations in 1939/40 based on records of 918 female fin whales. His work confirmed the earlier estimates of size at sexual and physical maturity, but he concluded that in the fin whale 13 corpora have been accumulated on the attainment of physical maturity. This discrepancy between Brinkmann's material and that of Wheeler (1930) and Peters (1939) who respectively found 15 and 14–15 corpora at physical maturity is readily explained by differing criteria of physical maturity, for this is rather a subjective observation. More recently, Japanese workers have obtained an even lower figure of 11·5 (Nishiwaki, 1950a, 1952). Brinkmann discussed 'corpus luteum accumulation as a clue to age determination'. He found similarities between the frequency distribution of corpora in his material and Wheeler's (1930), but did not come to any definite conclusions.

Laurie (1937) found a similar correlation in blue whales between the accumulation of 11–12 corpora and the attainment of physical maturity. He found no regular occurrence of maxima in his frequency distributions, but believed that comparison of certain features in the frequency curves for two successive years indicated an increment of slightly more than one corpus each year. By consideration of the fresh appearance of certain corpora he concluded that on average 1·13 were formed each *breeding season*, but then states that this is the *annual* increment. If ovulatory periods recur at 2-yearly intervals, then by this argument the annual increment should only be 0·57 corpora.

Ruud (1940, 1945) developed a new method of estimating the age of whalebone whales, based on the ridges present on the baleen. For 14 northern hemisphere fin whales he compared the number of

corpora in the ovaries with the results of baleen readings and found them to be in agreement with the findings of Mackintosh and Wheeler. He suggested that in the breeding season up to 6–7 ovulations are possible before pregnancy supervenes. In the light of these estimates of age he suggested that the age at sexual maturity was more likely to be 3 years than 2.

Mackintosh (1942) gave a valuable summary of all aspects of the biology of whalebone whales. He had little to add to the earlier work on reproduction and age, though in the light of accumulated data he made some slight amendments to the average lengths at sexual maturity. He was also able to give particulars of a very important whale mark recovered in 1941 which had been carried by a female fin whale for 6 years. The ovaries were recovered and had eight corpora. As there is no reason to suppose this whale was conspicuously immature when marked, he concluded that in this individual 'the rate of accumulation cannot have been much more than one a year (or two every 2 years), and, since there was no clue to the whale's age at the time of marking the rate of accumulation may have been even slower' (p. 227). On the other hand, if this female was immature when marked then the incremental rate could have been higher. This is hardly compatible with Wheeler's estimate, but it is in agreement with Peters's (1939) calculations.

Peters claimed that, as there was a very great difference in the development and activity of the corpus luteum of pregnancy and of ovulation, he had been able to establish morphological and histological criteria for distinguishing the corpora albicantia representing pregnancies and ovulations. By counting the former and assuming a 2-year reproductive cycle he provisionally estimated that in the fin whale there is an average of 1·8 ovulations in 2 years, and in the blue whale 1·9 ovulations. Consideration of his criteria, the colour and texture of the gland and the arrangement of the connective tissue trabeculae, suggest that he was confusing the various stages of regression (see below, p. 384). Nor is there such a marked difference between the corpora lutea of pregnancy and ovulation as he states. No other workers have been able to make such a distinction between the types of corpora albicantia in whales although this is well known in the cow (Hammond, 1927; Benesch and Wright, 1950), and is claimed for deer (Cheatum, 1949; Robinette, Gashweiler, Jones and Crane, 1955), but disputed by Golley (1957). In any case his estimates were based ultimately on only seven pairs of fin-whale ovaries and four pairs of blue-whale ovaries.

Robins (1954) has recently claimed that in the humpback whale (*Megaptera novaeangliae*) it is possible by morphological criteria to distinguish corpora lutea and corpora albicantia representing ovulations from those representing pregnancies. Dempsey and Wislocki (1941) believed that in this species restriction of the blood supply to the centre of the corpus luteum results in the formation of a central cavity. Robins suggested that this applied only to the corpus luteum of pregnancy, which is larger than the corpus luteum of ovulation (average 100–130 mm. and 80 mm. respectively), and claimed that the presence of a central cavity or, in corpora albicantia, a central core was diagnostic of a corpus of pregnancy. This hypothesis was based on a small number of ovaries and has not been confirmed. A basic assumption, that the formation of a cavity is a result of the large size of the corpus luteum of pregnancy, does not agree with observations on the incidence of cavities in fin- and blue-whale corpora lutea (see below, p. 359). Van Lennep (1950) studied the histology of blue- and fin-whale corpora and concluded that the corpora albicantia were persistent and that regression was completed in 3–4 years. He was able to find no constant differences between corpora associated with ovulation or with pregnancy, but made some suggestions about possible distinctions. Harrison (1949) and Sergeant (Anon., 1955) made histological observations on *Globicephala*, but were unable to distinguish the two types of corpora. Harrison stated that in this species only serial histological sections could be expected to give a precise indication of the number of corpora albicantia, which regress to become invisible macroscopically. Comrie and Adam (1938) made some observations on the ovaries of *Pseudorca*.

Japanese workers presented a vast amount of data in a series of papers on the results of their investigations (Nishiwaki and Hayashi, 1950; Nishiwaki and Oye, 1951; Mizue and Murata, 1951; Ohno and Fujino, 1952; Kakuwa, Kawakami and Iguchi, 1953). These followed the methods employed by Mackintosh and Wheeler (1929) and are in general agreement, though it is clear that no consistent pattern is present in the occurrence of maxima in the frequencies of corpora. They give average lengths at sexual and physical maturity, but there are variations and inconsistencies in their findings. As criteria of physical maturity they accept fusion of the epiphyses in mid-lumbar or thoracic regions and since fusion is in fact usually completed in the anterior thoracic vertebrae their estimates are necessarily low.

Ruud had shown that the ridges on the baleen plates could be used to estimate the ages of whales, though after the first few years wear at the tips was greater than replacement in the gum so that the method then gave minimum ages only (Ruud, 1940, 1945; Ruud and Jonsgård, 1950). The technique is to record and amplify the variations in thickness of the baleen plate by means of a suitable apparatus. In these recordings they claim to be able to distinguish annual steps or ridges associated with changes in the nutritive state of the individual. As long as the pattern diagnostic of the baleen laid down in lactation is present they feel they can be quite confident about the age. In his second paper, Ruud showed that the age of the fin whale at sexual maturity was more likely 3 years than 2. In the third paper it was shown that the blue whale also attained sexual maturity at later ages, averaging 5 years. In the first season of maturity slightly less than two ovulations occur and corpora subsequently accumulate at a rate of a little more than one a year; the maximum number of ovulations in any one period of heat appeared to be four. Hylen, Jonsgård, Pike and Ruud (1955) published the results of the examination of baleen plates from over seven thousand fin whales taken in the antarctic between 1945/46 and 1952/53. They state that they believe age groups O, I, II and III can be determined with great exactitude, because traces of suckling baleen can be recognized. In older groups there is some confusion, but they believe that the mistakes are few in group IV. Elsewhere (Hylen *et al.* unpublished report) they stated that sexual maturity in the female is attained in groups II–IV, averaging 4 years of age. A full account of the method is to be given in a later publication.

Tomilin (1940, 1945) also drew attention to the use of the ridges on the baleen plates for ageing whales and Nishiwaki in a series of papers (Nishiwaki and Hayashi, 1950; Nishiwaki, 1950*a*; 1950*b*; 1951; 1952) took up the problem. In the first two of these papers he drew attention to changes in the coloration of the crystalline lens of the eye. He measured the absorption of light by the lens (expressed as a percentage) using a photocell, and claimed that it increased regularly with age, as measured relatively by length, ovarian corpora, testis weight and physical maturity. This is not a very convincing piece of work, because large corrections are necessary to allow for the changes dependent on variations in the time post-mortem. Nevertheless, Nishiwaki (1950*a*) believed that it was more accurate and reliable than any other method of age-determination although it does not give a measure of absolute age. In the next two papers he takes up the question of ageing by means of the ridges in the baleen plates by Ruud's method and using his recording apparatus. He suggests that the average age at sexual maturity, which Ruud had placed at three years, should be four years, as Hylen *et al.* (unpublished report) later confirmed. He also suggests that four corpora accumulate each baleen period. Later (1951) he examined the rate of growth in length of the baleen by comparing the distance from gum to the first main ridge, with the length of baleen formed in the next period. This ratio he calls the growth index, which is expressed as a percentage of the latter period, and he calculates the weekly growth-rate during the whaling season. Assuming the growth-rate to be constant throughout the year he found that the annual increment was equivalent to one full growth-period. In a later paper Nishiwaki (1952) re-examined his data and combined the results of the work on the crystalline lens

with the baleen readings. He confirmed that the female fin whale attains sexual maturity at 4 years of age and the male at $3\frac{1}{2}$ years and used two large blue-whale foetuses to obtain an estimate of the degree of coloration of the lens at birth. He then calculated the annual increment in coloration of the lens from birth to sexual maturity (taking 4 years as the age at maturity) and applied this to the increase in coloration from sexual maturity to physical maturity to obtain an estimate of the length of this period, which he found to be approximately 6 years. He then assumes that two ovulations occur at sexual maturity and in the fin whale a further 9·5 up to physical maturity. Then the annual increment of corpora after the first year should be 1·5. The discrepancy between Nishiwaki's estimate of the number of corpora accumulated at physical maturity (11·5) and those of earlier workers (13–15) results from the use of different criteria as mentioned below, but this would not affect the result since it applies to both number of corpora and coloration of the lens. In the same way he obtains for the blue whale an average increment of corpora of 1·64 per year, and gives a table showing growth in length from sexual maturity up to 12 years. Although the figure of two to three ovulations per breeding cycle obtained by Nishiwaki agrees quite well with the conclusions put forward in the present paper, there are serious objections to his methods. The most important is the controversial nature of the evidence from the crystalline lens. Corrections are necessary to allow for the post-mortem changes, and the estimate of the degree of coloration at birth seems to be little more than a guess. Recent work both on baleen plates and on ear-plugs suggests that sexual maturity in the female fin whale is not attained until on average 5 years of age.

Since Mackintosh and Wheeler (1929) and Ommanney (1932) gave a general account of the reproductive tract, this aspect of the reproductive biology has received little attention, apart from an important paper by Matthews (1948). He demonstrated a well-marked cycle of change in the uterine mucosa from sexual immaturity, pregnancy, lactation, and anoestrus correlated with the state of the ovaries, mammary gland, etc. Post-partum involution is rapid and appears to occur without loss of the mucosa. Slijper (1949, 1956) also gives some information on the reproductive organs during pregnancy.

Relevant work on other species will be discussed later in this paper, but mention must be made here of a valuable series of papers on the humpback whale (*Megaptera novaeangliae*) by Chittleborough (1954, 1955*a*, 1955*b*, 1958) who was able to work on this species in the southern winter near its breeding grounds off West Australia.

When the present work began in 1954 the general outline of the biology of the fin whale had been established relatively unchanged since 1930. The female was assumed to be polyoestrous and various estimates of the rate of ovulation had been made, none of which could be accepted without reservations. No conclusive evidence of the complete persistence of corpora albicantia had been put forward and they could not be used as measures of age except in a very general way. The estimates of age based on baleen plates still required a final proof and could only be applied to young animals. The nature of the evidence from the crystalline lens was controversial.

Since then a new method of age-determination has been discovered by Purves (1955) and its value confirmed by Laws and Purves (1956), Nishiwaki (1957), Nishiwaki, Ichihara and Osumi (1958) and Purves and Mountford (1959). This depends on the presence of well-defined laminations in the ear-plug of whalebone whales which, once laid down, constitute a permanent record. Work on large collections of ear-plugs from antarctic fin whales is proceeding. This appears to confirm the figure for the annual increment of corpora albicantia given in this paper, but suggests that the ages at sexual maturity of both sexes are higher than previous workers have claimed.

The major part of the present paper concerns the female reproductive biology, and the work was carried out before the value of the ear-plug was known. Probably the most important confirmation of the value of the ear-plug for age-determination lies in the correlation which has been found between

the ages estimated from the ovaries and from the ear-plugs of a series of female fin whales. The value of this evidence depends on the completely independent nature of the two lines of work and for this reason and because they were not available when the work was carried out the ear-plug data will not be used in the first part of this paper.

MIGRATIONS

The growth-rates and mature sizes of northern and southern hemisphere fin whales are very different and the average annual cycle is 6 months out of phase, so we can take it that there is no important degree of interchange between them (Omura, 1950; Jonsgård, 1952; Pike, 1953), but the animals in both hemispheres do undertake long seasonal migrations. Kellogg (1929) summarized what was then known about the migrations of baleen whales. Most of this evidence relates to whales seen on passage in the northern hemisphere and reveals a movement from low to higher latitudes in spring and a return movement in the autumn. Mackintosh (1942) has also discussed the evidence for these migrations and concludes that it 'can leave no doubt that there is a general tendency for Blue and Fin whales to undertake long annual migrations between the Antarctic and temperate or tropical waters, though this is not to say that the Antarctic is completely deserted in winter or the warmer waters in summer' (p. 250). The humpback whale is a coastal species and migratory herds may regularly be seen from the coasts (Chittleborough, 1953; Dawbin, 1956 b). In the longitude of New Zealand the main herds are said to leave antarctic waters in early May, to reach 46° S. by mid-June, and to arrive at the breeding area at latitude 15° S. by mid-August.[1] On the return migration they reach 46° S. by early November and arrive at the feeding area about 66° S. by mid- to late December. The vanguard and rearguard reach the respective latitudes approximately 6–7 weeks earlier or later than the main group (Dawbin, 1956, p. 193). The fin whale is not a coastal species so direct observations of migrating animals are few and most of the evidence is circumstantial, but we may also reasonably draw analogies with the humpback whale. Some direct evidence comes from whale marking; 22 humpback whales marked in the antarctic were recovered off north-west Australia (Rayner, 1940), and a further nine in recent years, but so far there are only two marked fin whales to demonstrate the migration.[2] One marked in the antarctic in 64° 52' S., 22° 30' E. in February was recovered off Cape Province, South Africa, 33° 04' S., 17° 50' E. at the end of June 2 years later (Rayner, 1940); another was marked in October off the coast of Brazil in 28° 03' S., 46° 17' W. and recovered after 11 years near South Georgia in 52° 55' S., 38° 42' W. (Brown, 1954)[2]. Rayner and Brown established, as a result of marking returns, that these whales tend to return to the same antarctic locality and are partially segregated in certain broad areas though there is some lateral dispersal.

The indirect evidence comes from a number of sources. There is an important reference by Mörch (1911) to the occurrence of great numbers of fin whales along the Brazil coast, between 12° and 18° S. latitude every year from May to November, but this has not been confirmed. It is significant that whaling operations in the Antarctic have been largely confined to the period October–April with the largest catches obtained from December to March. In low latitudes off South Africa catches are made in the period May–October. This indicates that the bulk of the population spend the winter months in lower latitudes, and the summer in the Antarctic, but at one time catching was carried on throughout the winter at South Georgia, so not all migrate north in the autumn. Recently Brown (1957, p. 163) has found that 'not all rorquals go south for the southern summer and it may be that more than was thought either miss the southern migration altogether, or get out of step with the main migration movements'.

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[1] Chittleborough's work suggests mid-July off West Australia.

[2] Later mark recoveries have confirmed the humpback movements and Brown (1959, 1960) gives details of five additional fin whale recoveries.

Mackintosh and Brown (1956) examined the records of whales observed through an organized look-out system in the R.R.S. 'Discovery II', covering nearly 47,000 miles steaming in the Antarctic, and drew up a curve showing the variation in the size of the antarctic population of the larger baleen whales, month by month. This curve shows a maximum in February/March and a minimum in July/August and indicates that most of the population leaves the antarctic zone in winter. This curve represents the total numbers of blue, fin, and humpback whales, although a few sei whales may be included and some immature age groups are probably missing. From inspection of the antarctic catches and the variations in numbers calculated by Mackintosh and Brown it appears that fin whales spend an average period of about 4 months south of the antarctic convergence and that the main part of the population is south of the convergence from mid-December to mid-April.

The incidence of diatom infection on the skin of whales is indirect evidence of migrations (Hart, 1935) and suggests that while some individuals may spend the winter in antarctic waters almost all migrate to low latitudes in winter. Similar evidence is provided by the parasites which attack blue and fin whales in low latitudes and the partly explained presence of healed oval scars (Mackintosh and Wheeler, 1929; Mackintosh, 1942; Pike, 1951).

The chief contributing factors to the migrations of fin whales are undoubtedly food and temperature. Marr (1956) states that the main diet of the southern baleen whales consists of the crustacean *Euphausia superba*, known as krill, over 20 mm. long, and it appears that this size is very much more abundant in January, February and March than at other times of the year. The main concentrations of krill are confined to the East Wind drift in latitudes south of 60°–65° S. except in the Atlantic Sector where the Weddell drift brings a rich population into lower latitudes as far north as South Georgia (54° S.). The whales feed heavily on these populations of krill in summer and must feed but little in the warmer waters in winter. As a result, the animals in the winter catch at low-latitude shore stations show progressively decreasing blubber thicknesses and they are in poor condition when they move south in the spring. Once they are in antarctic waters the blubber thickness and oil production increase as the season advances (Ash, 1955, 1956).

Whales are mammals and maintain a body temperature of about 37° C. This implies that in cold waters more energy is expended to maintain this temperature than in warm waters. On average at the latitude of 62° S. the sea surface temperature is above −1° C. from December to June, but at 64° S. this temperature is exceeded only from January to April (Mackintosh, 1946), which is also the period when large krill appear to be abundant. When krill ceases to be abundant it is presumably disadvantageous for the baleen whales to be in cold waters and by moving to warmer regions they are able to reduce their energy expenditure while drawing on their reserves of fat.

The pattern of migration which has now been described applies to the population as a whole, but the movements of the different classes of fin whale differ in time and there are regular seasonal changes in the composition of the antarctic population from month to month. The sex-ratio tends to remain fairly constant, but Mackintosh (1942) suggests that the vanguard of the main herds of fin whales arriving on the whaling grounds in January is composed mainly of males and towards the end of the season females tend to be in excess of males. The percentage of immature whales in the catch increases towards the end of the season and the average length of the catch decreases. Wheeler (1934) showed that at South Georgia the average age declines through the season; the majority of physically mature females are taken in December, of sexually mature but not yet physically mature females in January, and the peak influx of immatures is in February. This is also true of the pelagic catch though the corresponding maxima occur rather later. The antarctic population of adult females also shows conspicuous seasonal variations in quality. Mackintosh (1942) showed that at South Georgia the percentage of adult females in the catch which were pregnant fell from 85% in October to 27% in

April, these figures being averaged over a number of years. A similar though less marked decline from December to March has been shown in the pelagic catch also by a number of workers (Mackintosh, 1942; Nishiwaki and Hayashi, 1950; Nishiwaki and Oye, 1951; Ohno and Fujino, 1952; Kakuwa, Kawakami and Iguchi, 1953). This is partly a result of the entry into the catch of resting females which were recently lactating and therefore protected and under-represented in the catch, but Ohno and Fujino (1952), Kakuwa, Kawakami and Iguchi (1953) and Laws (1959a) also suggest that pregnant females migrate northwards earlier than the others.

Ash (1955) showed how the rate of increase in blubber thickness was constant through the season and could be represented by a straight line; the curves describing the increase in oil content for two consecutive seasons (1953/54 and 1954/55) are nearly parallel, indicating that the rate at which whales lay down fat is independent of the store already there. He suggested that the variations about the regression lines representing blubber thickness and oil production might indicate waves of migration coming south, and points out that such waves of migration were observed by Mackintosh and Wheeler (1929) at South Georgia. In a later paper (Ash, 1956) he broke down the data on blubber thickness into separate figures for males, and for pregnant, non-pregnant and lactating females. He shows that males and non-pregnant females are represented by two curves which are almost identical, while the curve for pregnant females is well above, but nearly parallel to them, closely following the alterations in slope. He suggests that whales arrive in the Antarctic in groups which are made up of males, females which are pregnant and those which are not, and that these groups maintain their identity throughout the season. Ohno and Fujino (1952) have similar data.

We may conclude then, that fin whales undertake long seasonal migrations between the Antarctic and waters to the north. In the summer, largely from December to April, they are feeding on *Euphausia superba* in high latitudes and then move northwards to become dispersed over an immense area of ocean in winter, some to tropical waters and many in sub-tropical and temperate regions. It would appear that both the north and south migrations of older animals and of pregnant females are in advance of those of other groups and that the sexually immature animals are later.

THE OVARIES

For ovaries examined since 1954, drawings and records of the size and appearance of the ovaries, and the number, size, and appearance of the corpora lutea, corpora albicantia and follicles were made.

SIZE

No late foetal ovaries have been examined, but the average dimensions of four pairs of fixed ovaries from foetuses between 2 and 3 m. in length were: length 46 mm., breadth 17 mm., depth 12 mm.; the mean weight of single ovaries was 6·6 g.

Measurements of the dimensions of fixed post-natal ovaries are inaccurate because of distortion, but measurements were made on 131 pairs of fresh unfixed ovaries in the 1953/54 season.

Eight immature ovaries were of mean length 27 cm., breadth 8·2 cm., depth 3 cm.; 52 ovaries from non-pregnant mature females were of mean length 31·1 cm., breadth 11·4 cm., and depth 4 cm. Of 105 pairs of ovaries from pregnant females the ovary which contained the corpus luteum was of mean length 33·2 cm., breadth 12·1 cm., depth 4·2 cm. (excluding the corpus luteum) and for the other ovary the length was 32·3 cm., breadth 11·9 cm., depth 3·9 cm.

Weight is a better index of the size of the ovary and there are records of the combined weight of both ovaries for 1567 female fin whales from eight seasons between 1939/40 and 1955/56. The frequency distribution of combined ovary weights (in 0·5 kg. groupings) for these three classes of

animals are presented in Text-fig. 1. The records for immature females are not of course representative of the whole class of immatures, for, owing to the operation of the minimum length regulations, they include only those animals which are nearing sexual maturity. The intersection of the curves for immature and non-pregnant mature ovaries is at 0·6 kg. and for immature and pregnant ovaries at 0·95 kg., but owing to the wide variation in ovary weight near puberty there is a considerable overlap. Between immature and non-pregnant mature, the overlap is from 0·25 to 1·75 kg., and between immature and pregnant from 0·75 to 1·75 kg. It is not, therefore, possible to distinguish between all immature and mature females on the basis of ovary weight. The mean ovary weights for the different classes are shown in Table 1. The difference between the mean ovary weight of pregnant and non-pregnant mature females is both absolutely and proportionately much greater than Chittleborough (1954) noted for the humpback whale, and is statistically significant.
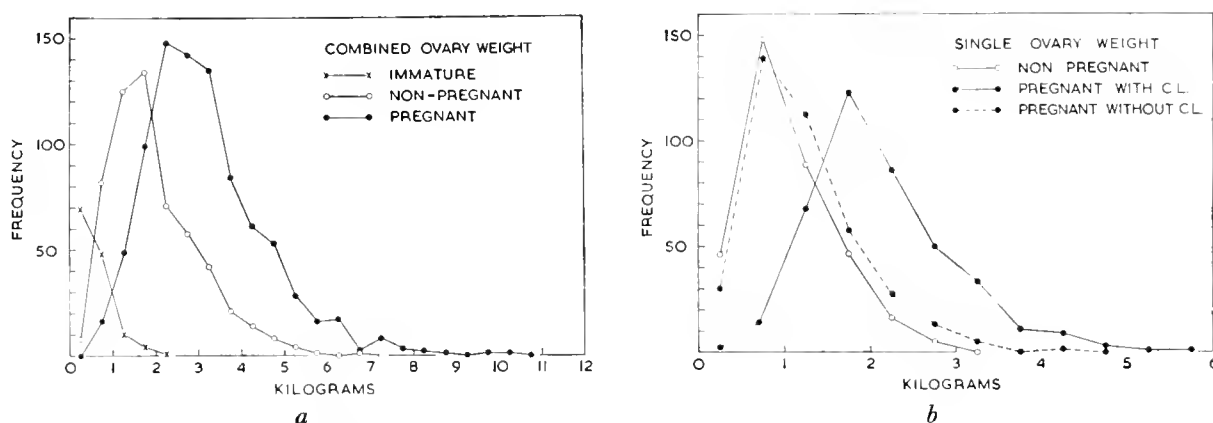
Text-fig. 1. Frequency distributions of ovary weights.

Table 1. *Summary of ovary weight records*

	Combined weight (kg.)		Single weight (kg.)	
Class	No. of pairs	Mean	No. of ovaries	Mean
Immature	132	0·97	—	—
Non-pregnant	569	1·97	352	1·04
Pregnant with corpus luteum	866	3·14	403	2·13
Pregnant lacking corpus luteum			391	1·24
Total	1567		1146	

The increased weight of the ovaries of pregnant females is only partly explained by the presence of the large corpus luteum. The mean weight of 372 corpora lutea was 0·88 kg. (see p. 357), and the ovaries of pregnant females weigh on average 1·17 kg. more than those of non-pregnant females. The discrepancy is probably to be accounted for by increased vascularization and increase in follicle size and numbers (see p. 348) which affects both ovaries of pregnant females.

In two recent seasons (1953/54 and 1955/56) 1146 mature ovaries were weighed separately. The frequency distribution is shown in Text-fig. 1 and the mean weights are set out in Table 1. These figures show that there is a mean difference of about 0·2 kg. between non-pregnant and pregnant ovaries without the corpus luteum, and a difference of about 0·89 kg. between the two ovaries of a pregnant female which is accounted for by the corpus luteum (mean weight 0·88 kg.).

Giant ovaries

Although the combined weight of a pair of fin-whale ovaries is usually less than 10 kg. and of blue-whale ovaries under 16 kg., there are two records of ovarian hypertrophy. One is of an 83-ft. pregnant blue whale with ovaries weighing in all 59·4 kg. (Laws, 1954). The other, previously unpublished, is a lactating female fin whale with ovaries together weighing 52 kg. (26 kg. each), which were examined at South Georgia in 1929. Both ovaries of this whale had a number of large bodies which appeared like hypertrophied corpora lutea; they showed a corona-like structure and several of them had a central cavity (see p. 359), but they were composed of white fatty tissues. There were four of these bodies in one ovary, of mean diameter 30, 25, 18 and 13 cm., and six in the other ovary measuring 23, 22, 21, 17, 11 and 8 cm. In the first ovary there were four corpora albicantia but no macroscopically visible follicles, and in the second ovary was a large protruding cyst 12 cm. in diameter.

In both examples of giant ovaries there was excessive fat deposition, but the blue-whale ovaries were otherwise normal. The fin-whale ovaries now described must be classed as pathological in view of the ten abnormal fatty bodies.

Morphology

The external appearance of the ovaries has been described and figured by Mackintosh and Wheeler (1929) and Ommanney (1932). In the foetus they are small, compact, tending to taper posteriorly with an irregularly grooved surface divided into a number of flattened lobes by branching sulci. In sexually immature females the ovaries elongate, and the smaller grooves gradually disappear so that the surface is smooth. Towards sexual maturity the development of Graafian follicles leads to the formation of rounded protuberances. In the adult the ovaries usually have a flattened elongated egg-shape, tapering posterior'y, with many rounded follicles and corpora albicantia protruding, the latter often attached by only a small area at the base. The corpora lutea usually project almost entirely from the body of the ovary and are sometimes connected only by a narrow neck. The colour of the ovary is a pink-grey-white, varying somewhat with the circumstances of death.

The ovary is reduced in thickness at the hilum, where it is attached to the mesovarium. Blood vessels and lymphatics enter and leave the ovary along this narrow connexion and the ovarian artery divides into a number of branches before entering the ovary. In a 68 ft. non-pregnant mature female there were respectively 15 and 16 arteries visible at the hilum of each ovary.

The medulla is a dense mass of white fibrous tissue supporting the many tortuous arteries, veins and large lymphatic sinuses. The larger arteries have a spiral configuration (Reynolds, 1950). A few branches pass into the cortical layer which invests the medulla up to the hilum. This cortex is 1–6 cm. in thickness and contains the developing and atretic follicles, the corpora lutea and corpora albicantia.

At the periphery of the cortex of sexually immature females under 60 ft. long a thin layer of cubical germinal epithelium rests upon a fibrous tunica albuginea which is already 150–250 μ thick. In sexually mature females no germinal epithelium has been found and the tunica albuginea is usually more than 1 mm. thick. The large follicles rest on the medulla and as they expand protrude from the surface of the ovary, filling the full thickness of the cortex. It is probable that the protrusion of the follicles and corpora as they mature is a consequence of the relatively rigid fibrous supporting nature of the cortex and medulla of baleen whales. In the odontocetes *Globicephala melaena* (Harrison, 1949), *Pseudorca crassidens* (Comrie and Adam, 1938), and *Physeter catodon* (Matthews, 1938a), the ovary accommodates the growing follicle or corpus luteum so that the latter remains for the most part invested by cortical tissue and the ovarian surface is smooth. In some fin-whale ovaries there are a few small stalked mushroom-shaped bodies of fibrous tissue projecting from the hilus or from the ovarian surface.

Laws (1957) examined the distribution of corpora albicantia and corpora lutea in 394 fin-whale ovaries and found the probability that the corpora are not randomly distributed to be highly significant. For 30 ovaries for which the orientation was known 74·1% of the total corpora were in the anterior half. In 32·7% of ovaries with two or more corpora they are entirely confined to the anterior half of the ovary. The position of the corpora in relation to the long axis of the ovary was measured in 96 fin-whale ovaries. This shows a progressive decline in the frequency of corpora at increasing distances from the anterior pole, and they are completely absent from the posterior third of the largest ovaries.

RELATIONS

Ommanney (1932) has described the position of the ovaries in relation to the reproductive tract in the foetus. An adult female and an immature female have been examined closely in connexion with the present study and will be briefly described.

In the foetus the ovary lies free on the broad ligament and the triangular fibrous sheet extending from the ovarian funnel does not cover the ovary (Ommanney, 1932, figs. 12 and 13).

One ovary of a 75-ft. pregnant female weighed 1·6 kg. and measured 27 × 12 × 4 cm. It bore a corpus luteum, weight 0·7 kg., diameter 10·3 cm., and three large corpora albicantia. The other ovary weighed 0·65 kg. and measured 25 × 12 × 3 cm., but had no corpora. The transparent fibrous sheet extending from the ovarian funnel was rhomboid in shape and measured 60 × 50 cm., the longest axis stretching from the anterior pole of the ovary to the uterine horn. The ostium abdominale was situated just anterior to the intersection of the two main axes. The edges of this sheet were free except where it was attached by a short ligament in the vicinity of the anterior pole of the ovary, and by a longer and more slender ligament medially to the uterine horn; in contrast to the foetus it was not attached to the posterior pole of the adult ovary. This sheet is normally folded lengthwise so that it invests the anterior part of the ovary and is attached to the broad ligament along the line of this fold. It corresponds to the funnel-shaped pouch described by Harrison (1949) in *Globicephala melaena*, and as in that species the inner aspect is lined by numerous membranous ridges running inwards to the ostium, which is lined by ciliated fimbria. The short ligament attaching the anterior end of this pouch was not observed to continue to the ostium abdominale in this specimen as described by Daudt (1898) and Ommanney (1932). An immature female 61 ft. in length had ovaries 24 × 5·2 × 2 cm. in size; the relations of the ovary were similar, but the pouch differs somewhat from that of the pregnant female. It over-arched the anterior two-thirds of the ovary and resembled the bursa ovarii of the dolphin *Stenella* figured by Burne (Fraser, 1952, fig. 33) or the 'delicate arched covering or pavilion' of *Globicephala* (Murie, 1873). In this immature female a conspicuous fimbriated groove extended from the anterior pole of the ovary to the foremost edge of the ostium abdominale. This was described by Ommanney (1932), but was not observed in the pregnant female described above.

The Fallopian tube lies on the broad ligament partly covered by the ovarian sac. In the pregnant female it was 61 cm. in length when straightened out. At the ostium abdominale the diameter of the lumen was 4·0 cm.; at a distance of 20 cm. from the ostium it was 1·5 cm. in collapsed diameter and lined by numerous longitudinal folds, and a further 20 cm. from the ostium it had narrowed to 4 mm. and had four longitudinal folds. For the first two-thirds of its length it was sinuous, and then almost straight; where it entered the uterine horn there was no papilla or constriction. The Fallopian tube of the immature female measured 49 cm., the first 22 cm. next to the ostium being much folded and the remainder more direct. The lumen was 1·75 cm. in diameter at the ostium, 1·25 cm. at a distance of 10 cm. from the ostium, 1·05 cm. at 20 cm. distance and 0·3 cm. at 30 cm. distance. For the first half the epithelium was much folded, but regular longitudinal folds appeared in the second part.

From the anterior pole of the ovary a large fold, the plica diaphragmatica, runs lateral to the

kidneys and forwards to the diaphragm; a large pink-coloured lobe of fatty tissue arises from this fold near to the anterior pole of the ovary. In the pregnant female it measured $42 \times 25 \times 10$ cm. and in the immature female about $33 \times 21 \times 7$ cm. This reddish-pink fatty lobe is very conspicuous against the grey-white peritoneum and serves as a useful landmark when searching for the ovaries on the flensing deck. Rounded fatty lobes have also been noticed in the broad ligament.

From the posterior pole of the ovary two conspicuous ovarian ligaments extend, one to the uterine horn and the other along the broad ligament. In addition a broad fold representing the mesovarium runs over the broad ligament carrying most of the blood vessels, lymphatics and nerves to the ovary.

The differences between this account and the description given by Ommanney (1932) are the result of comparing the foetal anatomy with the adult. The most important respect in which they differ is the development of the ovarian sac in the sexually immature and adult female, whereas in the foetus the ovary 'lies free on the ligamentum latum and is not enclosed in any sort of sac or pavilion' (Ommanney, 1932, p. 444).

GRAAFIAN FOLLICLES

FOETAL OVARIES

Chittleborough (1954, pl. 1) found abundant primary follicles up to 0·13 mm. in diameter in ovaries from near-term humpback-whale foetuses 4·54–4·66 m. long. The average neo-natal length in this species is 4·56 m. (Chittleborough, 1958).

The neo-natal length of fin whales averages 6·4 m. (Laws, 1959b) and of 956 foetuses of known length in the present material none was above 6·0 m. Only 0·9% are above 4·0 m. and only 0·4% above 4·5 m. This is a result of sampling being restricted to a period when most females are in mid-pregnancy, whereas Chittleborough's sample are in early or (the majority) in late pregnancy. Consequently no near-term fin-whale foetal ovaries are available for examination. All foetal ovaries examined including the largest, from foetuses measuring 3·8 and 4·16 m., show as yet no development of primary follicles. The genesis of follicles must, therefore, begin in the last 2 or 3 months of gestation as in man.

IMMATURE OVARIES

Owing to the minimum size regulations for the antarctic pelagic catch in recent years only the larger immature females are sampled.

The cortex of two pairs of immature ovaries from females of length 54 and 56 ft. which have been sectioned for histological examination contained very numerous primary follicles, most of which were from 45 to 70 μ in diameter. These are already separated from the germinal epithelium by a tunica albuginea which is about 150–250 μ in thickness (Pl. IV, fig. 6).

The size frequency distribution of the largest follicle in 80 pairs of immature ovaries in the material is shown in Text-fig. 2. The majority, 66%, are less than 1 cm. in diameter; only 17·5 and 8·8% are over 2·0 and 3·0 cm. respectively, the largest being about 5 cm. With few exceptions these follicles appeared to be atretic with thick elastic walls, and when a sample was examined histologically it was confirmed that they were in varying degrees of atresia.

One immature female examined in 1954 (on 10 February, length 68 ft.) had ovaries of unusual appearance. The body of each ovary was very thin and strap-like, measuring $22 \times 6·5 \times 1·5$ cm. and $26·5 \times 5·5 \times 1·0$ cm., the corresponding weights being 0·4 and 0·3 kg. Each ovary had several large follicles projecting from the surface and often connected only by a small neck. The largest were 3·5 and 2·7 cm. in diameter. These follicles had very thin transparent walls in which the blood vessels were very conspicuous. In view of their relatively small size and lack of turgidity it seems unlikely

Table 2. *Immature fin whale females approaching puberty: mean maximum follicle diameters*

Month	Size of sample	Mean max. follicle size (mm.)		S.E.
		Monthly	Grouped	
January	20	10·8	—	2·25
February	14	10·6	—	1·71
March	12	5·0	—	†
April	3	6·0 ⎱		
May	2	6·0 ⎰	6·0	2·69
June	2	29·5 ⎱		
July	1	30·0 ⎰	29·66	2·12
August*	4	32·5	—	2·17
October	1	25·0 ⎱		
November	3	33·0 ⎰	31·25	5·69

* 61–63 ft. in length.
† The March sample values are all recorded as about 5 mm.
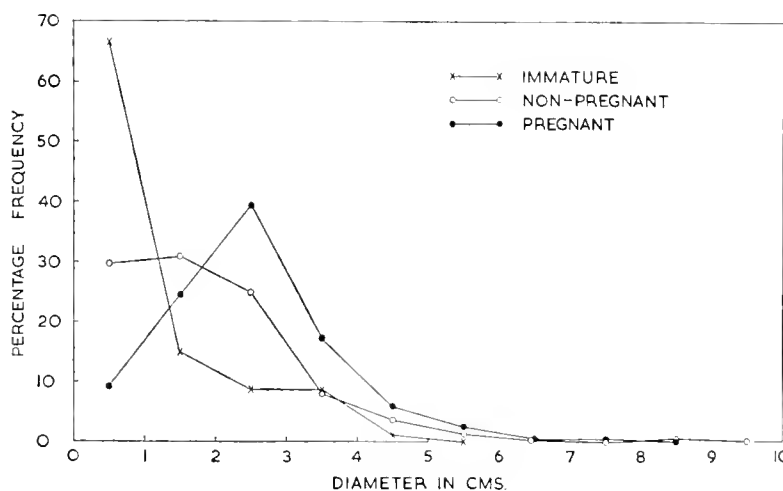
Text-fig. 2. Frequency distributions of maximum follicle diameters.

that these were maturing follicles, but they may have reached a stage of development at which regression was about to begin.

Mackintosh and Wheeler (1929) showed that the size of the largest follicle in female fin whales approaching puberty increased from a minimum in January–April, to about 3 cm. in June and July. There are in the present material 62 pairs of ovaries from immature females which were approaching puberty (defined as females over 63 ft. in length, except for four immature females taken at Durban which were 61–63 ft. in length). In Text-fig. 3 the means and variation of seven samples from January, February, March, April and May combined, June and July combined, August, October and November combined, are presented. The June/July sample is from Saldanha Bay, South Africa, and the August sample is from Durban, South Africa. Although the size of the critical samples is small, this evidence suggests that there is a follicular cycle showing one or more peaks from June to November or December, when the maximum follicle size is about 3 cm. or more, and minimum values between December (or January) and May, when the maximum follicle size is about 1 cm. or less. The absolute maximum size, from an immature female taken in November, was about 5 cm.

This agrees with conclusions about immature humpback whales based on material collected in the breeding season of this species. Chittleborough (1954) states that immature females with follicles at

or above 3 cm. in diameter are maturing and approaching the first ovulation. The fin-whale material shows that in most mature females and in some immature females, follicles above 3 cm. may be in cystic atresia. The present evidence suggests that immature fin whale females may be approaching the first ovulation in June, July, August, October, November and possibly September and December.
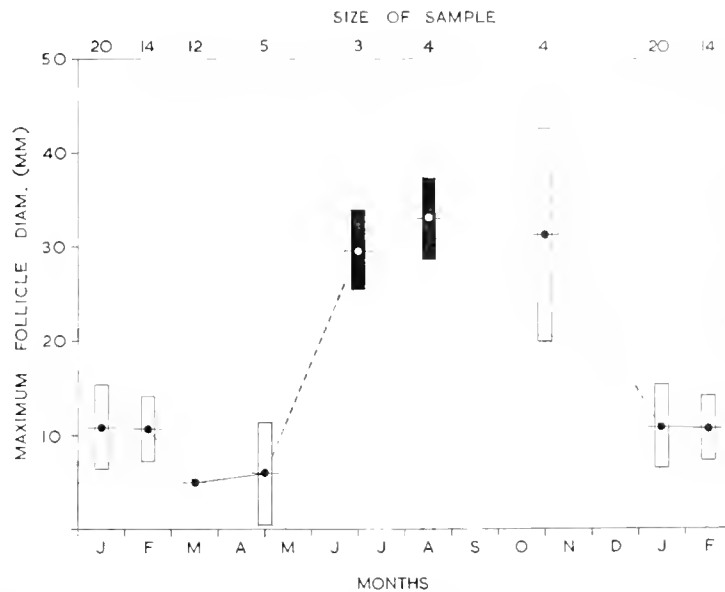
Text-fig. 3. Monthly mean size of largest follicle in 62 pairs of ovaries from immature females which were approaching puberty (mean ± 2 s.e.; black, South Africa; white, Antarctic).

Adult ovaries

Primary follicles

Laws (1957) stated that in adult fin-whale ovaries the tunica albuginea is from 0·95 to 1·6 mm. in thickness and that no primary follicles had been seen in histological preparations. Since then very small numbers of primary follicles have been observed in the ovaries of two mature fin whales, one of length 73 ft. in anoestrus, and one of 70 ft. pregnant with a foetus 2·79 m. long. These primary follicles are very few and scattered in distribution and their absence in other mature females examined is probably more apparent than real. For instance, the average surface area of one ovary of a non-pregnant mature female is about 800 sq. cm. and it would be a major task to sample even one pair adequately. Usually only one or two samples representing 0·1–0·3% of the surface area are embedded and in a large series it is impracticable to examine more than about one-tenth of this material histologically, so that less than 0·05% of the cortex is searched. The large size of the organ is a very real handicap in any studies of the finer details. It is probable, however, that the numbers of primary follicles decrease greatly with age. In the rabbit, for instance, Desaive (1941) found that these decreased from 120,000 at 3 months to 6000 at 18 months.

'Recently ovulated' females

There are records of the diameter of the largest follicle in 23 recently ovulated fin whales taken in the Antarctic, most frequently in November–December. These may be characterized as females which had a large and apparently normally active corpus luteum in the ovaries, but in which an intensive search of the uterus failed to reveal a foetus. Four pregnant females with a foetus less than 4 cm. long are also included in this group. The correctness of the diagnoses of recent ovulations is confirmed by the data set out in Text-fig. 4. Thus, in pregnant females considered as a whole, the mean maximum

follicle size is 2·78±0·15 cm. and the recently ovulated class of females has a mean maximum follicle size of 3·8±0·53 cm. This statistically significant difference disposes of the possibility that the 'recently ovulated' females were pregnant females in which a foetus had been missed in the search, or even pregnant females which had aborted their foetus when harpooned. It is, however, possible that very small embryos could have been overlooked in some of them. The occurrence of recently ovulated females in summer in the Antarctic is a fact which is of great importance in establishing the nature of the annual reproductive cycle in the female fin whale (p. 436).

Chittleborough (1954) does not give figures for the size of the largest unruptured follicle in the ovaries of humpback females after ovulation. He gives (in his fig. 3) maximum follicle sizes for females approaching ovulation, which by his definition are females in which the largest follicle is over 3 cm. in diameter. For 38 females with follicles over this critical diameter the mean maximum follicle size is 4·4 cm., and the largest follicle, at 10·5 cm., was close to the time of rupture. One pair of ovaries had maturing follicles measuring 53, 37, 35, 34 and 30 mm.

Pregnant females

It has been pointed out that most of the females in this class which have been examined are in mid-pregnancy (with foetuses 0·5–3·0 m. in length). The frequency distribution of the diameter of the largest follicle in 341 pairs of pregnant ovaries is shown in Text-fig. 2, the mode being 2·5 cm. and the mean 2·78±0·15 cm. This is in contrast to the condition in humpback whales in late pregnancy in which the mean diameter of the largest follicle in 45 pairs of ovaries is 6·4±0·9 mm. (Chittleborough, 1954). There are very few records from fin whales in the last quarter of pregnancy and the diameter of the largest follicle in lactating whales (1·93±0·34 cm.) although smaller than in pregnant females is not as low as in late-pregnancy humpbacks. However, in the Antarctic the majority of lactating fin whales taken are in *late* lactation (p. 446).

The records from pregnant females can be subdivided according to the foetal lengths so as to give an indication of the variation in follicle size during pregnancy. This has been done for 341 females and the result is given in Text-fig. 4, which shows the range, mean and twice the standard error of the mean for each foetal length group. In the 0–0·5 m. group four records from foetuses of length 4 cm. or less have been removed to the 'recently ovulated' class. Out of 23 records for the 4–6 m. length group, two are of maximum follicle diameters of 7 and 8 cm. These are clearly separate from the remaining records and if used they introduce a heavy weighting; they are thought to be abnormally persistent large cystic follicles and in calculating the mean size they have been rejected. Only two records of follicle size from females with foetuses over 5 m. are available; the largest follicles were respectively 8 cm. (mentioned above) and 2 cm. in diameter.

The mean maximum diameter decreases from 3·8±0·53 cm. in recently ovulated females to 2·53±0·3 cm. in the first few months of pregnancy, then appears to increase to 3·12±0·28 cm. at mid-pregnancy followed by a decrease to 2·07±0·42 cm. about 1 month before parturition. With the exception of recently ovulated females the values for the mean ± 2 s.e. overlap, owing to the variability in follicle size, but the maximum values and the percentage of records over 3 cm. (Text-fig. 4) also follow this pattern, so it probably represents a real cycle in follicle activity, with a period of about 5–6 months. Such follicular cycles are known during pregnancy in other mammals and are usually of the same period as the dioestrous cycle (see p. 352). Usually the follicles enlarge but enter cystic atresia before maturing, but in some species ovulation takes place with the production of accessory corpora lutea. It is unfortunate that there is no material from late pregnancy for the fin whale, but it is impossible to ignore the evidence concerning follicle size in late-pregnancy humpback whales, because in other respects the two species have so many features in common. The values for late-

pregnancy humpback whales have, therefore, been inserted in Text-fig. 4 at a foetal length corresponding to late pregnancy in the fin whale.

Another factor which must be mentioned is that in mature blue and fin whales the diameter of the largest follicle is proportional to the body length (Nishiwaki and Oye, 1951; Nishiwaki and Hayashi, 1950). It is shown later (p. 411) that older mature females are in advance of younger mature females in their sexual cycle and, therefore, have the larger foetuses at any one time. In the material under consideration, which is limited in time to a few months, the average maternal age and the average maternal body length increase with increasing foetal length. In accordance with the findings of the Japanese workers there would, therefore, be a bias towards larger follicle diameters in the second half
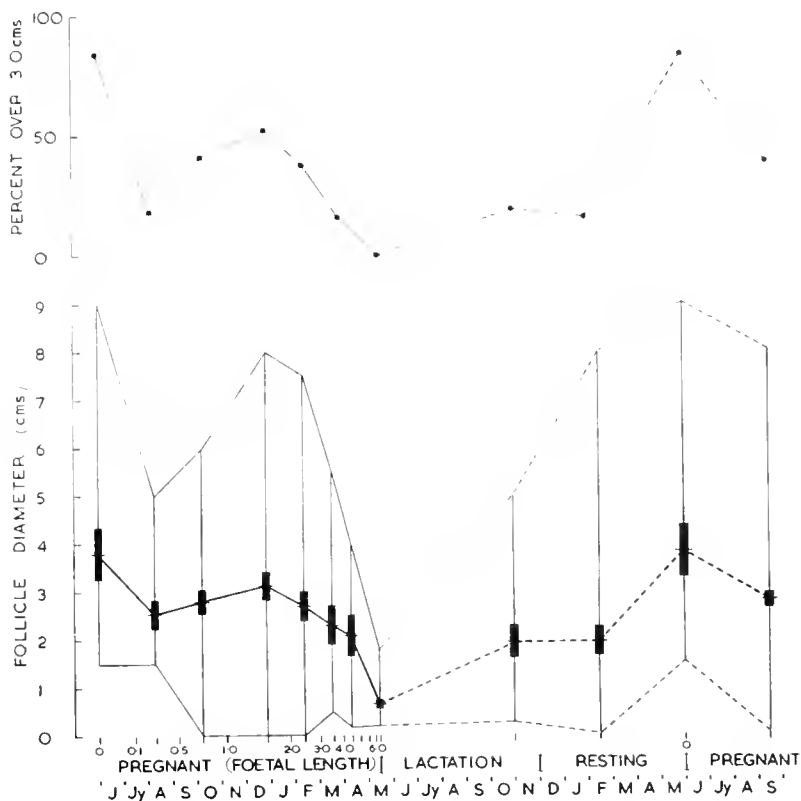
Text-fig. 4. Follicular activity at different stages of 2-year cycle. Above, percentage of follicles over 3 cm. in diameter; below, size of largest follicle (mean ± 2 S.E., and range; near-term values from humpback whale).

of pregnancy. If allowance is made for this there is an even greater decline in follicle size during the second half of pregnancy in individual females, which gives a closer agreement with the findings for late-pregnancy humpback whales.

Lactating females

Owing to the regulations prohibiting the taking of lactating whales and the small numbers entering antarctic waters, follicle records from only 56 lactating fin whales are available. The majority of these females would be in late lactation (see p. 446). They show a mean maximum follicle diameter of 1·93 ± 0·34 cm. and a range from 0·5 to 5·0 cm. Chittleborough (1954) gives the range of maximum follicle diameter for 60 humpback whales in late lactation as 1·0–5·0 cm., which is in very close agreement, especially since some of the fin-whale records may be from females in mid- or early lactation. (It is not possible to estimate the stage of lactation of individuals.) For three humpback whales in mid-lactation the largest follicles are 1·1, 1·5 and 1·8 cm. and for three in early lactation the maximum follicle sizes were 0·6, 0·8 and 2·6 cm. respectively. These were probably in very early

lactation because the corpus luteum was still large (97 mm.) and in gross appearance similar to the corpus luteum of pregnancy. Of the humpback females in late lactation 18% had maturing follicles (diameters 35–50 mm.) or had recently ovulated. Of the lactating fin whales 19·6% had maximum follicle diameters of 35–50 mm. and five had recently ovulated (see Table 19, p. 430). Such close agreement might be taken to suggest that the larger follicles in late-lactating female fin whales may be approaching ovulation, but it is also possible that some follicles are regressing after a former period of activity, as appears to be the case in the second half of pregnancy. Gross and histological examination suggests that the majority of graafian follicles in fin whales taken in the Antarctic are in atresia, but that some are apparently healthy.

An examination of follicle sizes in earlier and later phases of the sexual cycle throws some light on this point. We have seen that in the second half of pregnancy follicle size was declining (expressed as absolute maximum size, mean maximum size and percentage above 3 cm.), and from late pregnancy to late lactation there is an increase in follicle size. The six records from early and mid-lactation humpback whales are not sufficient to permit any firm conclusions, but in view of the probable follicle size in late pregnancy the 2·6 cm. follicle in early lactation is suggestive of post-partum follicular activity. In the fin whale, considering follicle size alone, either there is a period of follicular activity at some time between parturition and late lactation, or the follicles in late lactation are maturing, or both possibilities obtain.

As regards the first alternative 15 lactating fin whale females were simultaneously pregnant (p. 430). The mean foetal length is 1·69 m., which corresponds to a foetal age of about 7 months and means that the current pregnancy began very soon after the termination of the previous pregnancy. It appears likely that nearly all lactating females have a post-partum ovulation but that, owing to the physiological demands of lactation, the majority fail to conceive an embryo. Evidence confirming this view is presented in a later section of this paper (p. 430).

The second alternative is discussed in the following section. The evidence of five late-lactation females which had recently ovulated is highly suggestive.

' Resting' females

'Resting' females are here defined as mature females which are not pregnant, not lactating and not recently ovulated (that is, with corpus luteum), but some of them appear to be approaching ovulation, or to have ovulated fairly recently. The mean maximum follicle diameter of this group is 1·93 ± 0·29 cm., which is virtually identical with the figure for lactating females. The mean maximum follicle diameter for 'resting' humpback whales is 2·0 cm. (Chittleborough, 1954) although by definition this is not a directly comparable group.

Four considerations suggest that this class of fin whales undoubtedly includes some females in pro-oestrus or recent post-oestrus. First, the 'resting' condition is usually the state preceding pregnancy (except for post-partum conceptions). Secondly, it embraces the 'recently ovulated' class, because ovulation succeeds dioestrus (or anoestrus) and pro-oestrus, and is in turn succeeded by pregnancy, dioestrus or anoestrus. Thirdly, if we accept as the criterion of current or recent follicular activity the possession of follicles over 3 cm. in diameter, then 16% are or have recently been active. Fourthly, the largest follicle in this group was 8 cm. in diameter, as compared with 5 cm. in late lactation.

Evidence will be presented later in this paper (p. 436) showing that there is in fact an ovulatory period at the transition from lactation to 'resting' anoestrus. This explains the range of follicle diameters which is found and also the existence of a class of 'recently ovulated' females in antarctic waters during the summer months.

Ovarian cysts

Cystic follicles are of common occurrence in the ovaries of fin whales taken in the Antarctic and may be up to 9 cm. in diameter.

Other cyst-like structures also occur, very infrequently, and may be termed 'ovarian cysts'; they are aberrant cystic follicles and it is difficult to find an exclusive definition for them. Usually, they may be distinguished from true cystic follicles because their walls are either unusually thin or unusually thick, and the contents may be either fluid, gelatinous, or paste-like. Out of over 2000 ovaries, ovarian cysts occurred in three immature females, 11 pregnant, eight 'resting' and one lactating female.

The largest, from an immature female, was fluid-filled, 35·5 cm. in mean diameter, and weighed 4·3 kg. It was thick-walled and abundantly supplied with blood vessels. Another, from a 'resting' female was 16 cm. in diameter and weighed 0·9 kg. Other large cysts were from a lactating female (20 cm.) and three pregnant females (14, 20 and 21 cm.). The smallest, from a pregnant female, was 2 cm., fluid-filled, with a fibrous wall 8 mm. thick. Four cysts from 7 to 20 cm. in diameter had either fluid or gelatinous contents and a peripheral layer of luteal tissue 7–10 mm. thick. Two of these were from 'resting' females and two from pregnant females. The abnormal fin-whale ovaries containing 10 bodies superficially like corpora lutea, but composed of white fatty tissues and measuring from 8 to 30 cm. in diameter, have already been mentioned (p. 343). On one of these ovaries there was a 12-cm. fluid-filled cyst. One 5·4-cm. cyst from a 'resting' female was similar in external appearance to a corpus luteum, but contained a thick brown paste. Follicles with a cellular internal structure, like an agglomeration of bubbles, are occasionally seen.

Conclusions

There are insufficient data from the examination of the follicles of fin whale females taken in the Antarctic to establish the variation of follicular activity during the lactation and 'resting' phases of the annual cycle, but what little there is suggests that there is a period of follicular development in early lactation and another immediately after lactation. In the humpback whale, in which lactation is prolonged over 10½ months, this post-lactation ovulation usually coincides with the male sexual season and initiates the next pregnancy.

An observation by Chittleborough (1958) is of especial interest in connexion with a possible post-partum ovulation period. In one pregnant humpback female in late pregnancy (foetus 3·92 m.) the follicles had developed considerably and one follicle, 48 mm. in diameter, was maturing. The corpus luteum of pregnancy was in the early stages of resorption, similar in size and structure to the condition normally found during early lactation. This condition is rare; in over 70 other females during advanced pregnancy there was no such marked resorption of the corpus luteum and no follicular development. This exception strongly suggests that when the suppressing effect of the corpus luteum and placenta is removed after parturition, there may be a post-partum follicular cycle. Marshall and Moir (1952) review work in this field and show that the oestrogen content of blood and urine in the human female increases during the second part of pregnancy to a maximum just before parturition. The concentration rapidly falls at parturition so that after 3–4 days it has reached the level for non-pregnant females. This oestrogen is mainly secreted by the placenta. It is well known that oestrogen suppresses follicular growth.

The data from pregnant females lends itself more readily to treatment because it is possible to subdivide the sample and compare the variation in follicle sizes over a period of 11 months. It is then apparent that there is a single cycle of follicular development during pregnancy. It is now generally

4

accepted that in mammals follicular activity is limited but not necessarily suspended during pregnancy, because the secretion of progesterone by the corpus luteum prevents pre-ovulationary differentiation and causes cystic atresia (Gillman, 1941; Van der Horst and Gillman, 1945, 1946).

It is well known that in the rat there are oestrous cycles during pregnancy (Long and Evans, 1922; Nelson, 1929; Swezy and Evans, 1930; Swezy, 1933). The follicular development proceeds only up to a certain point, when cystic atresia begins, and corpus luteum cysts sometimes form, the granulosa degenerating and the theca interna luteinizing. Similar luteinized cysts are occasionally found in whale ovaries (p. 351). In the guinea-pig (Bujard, 1953) the percentages of growing follicles at different stages of pregnancy are indicative of four oestrous cycles. In *Elephantulus* (Van der Horst and Gillman, 1945) there are three phases of follicular growth during pregnancy; in early pregnancy small cystic follicles form, which are replaced by large cystic follicles and they in turn by small cystic follicles. In some pinnipeds Harrison, Matthews and Roberts (1952) found two periods of follicular stimulation after implantation of the blastocyst. In the elephant seal, *Mirounga leonina*, Laws (1956c) found one period of follicular growth during the free blastocyst stage and another follicle cycle just after implantation.

Williams, Carrigus, Norton and Nalbandov (1956) observed mating by ewes in early and late pregnancy. Heats during pregnancy were not accompanied by ovulation in the animals which were killed to check on this point. They found a significant increase in follicle number and follicle size from early pregnancy up to the 25th day of pregnancy; during the remainder of pregnancy the follicle number remained constant, but follicle size decreased significantly.

The follicular activity in the fin whale during pregnancy is at a maximum at mid-pregnancy which is, for the average female, in November/December. Elsewhere (p. 450) it is shown that the fin whale is probably seasonally monoestrous with peak ovulatory periods in June–July and November–December. It seems probable that the follicular cycle during mid-pregnancy in the female fin whale represents a suppressed oestrous cycle as for example in the rat, guinea-pig and sheep.

In some mammals ovulation is of regular occurrence during pregnancy. In the mare, for instance, the corpus luteum of pregnancy regresses after about 30 days and is replaced by a set of accessory corpora lutea by the luteinization of all follicles with antra, the larger of which ovulate (Asdell, 1946; Amoroso, Hancock and Rowlands, 1948). Similarly in the elephant, *Loxodonta africana*, further corpora lutea are formed during pregnancy (Perry, 1953); in the rodent, *Lagidium peruanum* (Pearson, 1949) and in the porcupine, *Erithizon* (Mossman and Judas, 1949) accessory corpora lutea form during pregnancy. Hansson (1947) showed that in mink (*Mustela vison*) oestrus, mating and ovulation can occur during the free blastocyst period, and recently Harrison and Neal (1956) and Neal and Harrison (1958) have shown that the badger (*M. meles*) may have up to 9 months delay in implantation during which as many as three ovulations may take place.

Although the fin whale has a follicular cycle during pregnancy there is no evidence that ovulation ever occurs during pregnancy. There are a number of primiparous females in the present material which have only ovulated once and many of these are in late pregnancy, in lactation, or post-lactation. In these animals it is certain that no ovulations can have occurred during pregnancy.

THE CORPUS LUTEUM

Corpora lutea are normally formed from all ruptured follicles, but usually they soon degenerate if fertilization of the ovum and implantation do not occur, and are then referred to as corpora lutea of the cycle or corpora lutea of ovulation. The life-span of the corpus luteum of ovulation in different species is remarkably uniform and independent of body size. 'The range of variability encountered is about 10–20 days (the upper limit being represented by the cow), but in the great majority of animals

it is probably of the order of only 10–15 days' (Eckstein, 1949, p. 400). In some mammals the corpora lutea of ovulation are short-lived and probably non-functional, but they can be activated by a copulation which does not result in pregnancy, or by mechanical stimulation of the cervix. They may then persist longer and are called corpora lutea of pseudopregnancy. With the exception of some carnivores and marsupials pseudopregnancy appears to be largely confined to the rodents.

There is no evidence of pseudopregnancy in any of the cetaceans which have been studied and it is unlikely that this condition occurs in whales, as it could hardly have passed undetected. It is here assumed that the corpus luteum of ovulation in the whale conforms to the generalization made by Eckstein (1949) and that it persists in a recognizable form for less than a month, probably for about 15–20 days.

If fertilization and implantation occur the corpus luteum persists for a long period as a corpus luteum of pregnancy. In the whale this period covers the duration of pregnancy, but in some mammals the corpus luteum degenerates before the end of pregnancy, or may be replaced by a set of accessory corpora lutea as in the mare and elephant (Amoroso, Hancock and Rowlands, 1948; Perry, 1953).

Accessory corpora lutea are usually defined as corpora formed as the result of luteinization of an unruptured follicle at the same time as the normal corpus forms, whether it be a corpus luteum of ovulation, or of conception. In the mare during pregnancy a set of corpora are formed by the luteinization of all or nearly all the follicles with antra; the larger follicles ovulate, the smaller luteinize (Amoroso, Hancock and Rowlands, 1948). In the elephant the accessory corpora also form from either ovulated or unovulated follicles (Perry, 1953). Accessory corpora lutea in the Norway rat form by luteinization of unruptured follicles (Hall, 1952). In histology and function they appear to be identical, whatever the mode of formation. Brambell (1956) uses the term accessory corpora lutea as synonymous with corpora lutea atretica, for certain animals, but there is an important difference which he points out earlier. The corpora lutea atretica form from medium and large unruptured follicles by 'hypertrophy and hyperplasia of the cells of the theca interna after the degeneration of the membrana granulosa'. The luteal tissue in true corpora lutea is derived from the membrana granulosa.

In the present account the term 'accessory corpus luteum' is used to describe corpora formed at the same time as a corpus luteum of pregnancy or a corpus luteum of ovulation, whether derived from ovulated follicles or from unruptured follicles. In the case of a multiple ovulation when there are only one or two foetuses and more than one or two of the corpora have rupture points, the largest are assumed to be corpora lutea of conception and the others are classed as accessory corpora lutea of pregnancy. Similarly when there is a multiple ovulation without conception, the largest ruptured follicle is assumed to be the corpus luteum of ovulation and the others, whether ovulated or not, are termed accessory corpora lutea of ovulation. In the fin whale there is no evidence for the formation of accessory corpora lutea during pregnancy, as in the mare, elephant, viscacha, and porcupine (Amoroso, Hancock and Rowlands, 1948; Perry, 1953; Pearson, 1949; Mossman and Judas, 1949), and this is not a regular feature of pregnancy in the whale. In any case accessory corpora lutea only comprise 3–4% of all corpora lutea.

FORMATION OF THE CORPUS LUTEUM

The humpback whale is the only species of baleen whale which has been extensively studied in the breeding season and it is convenient to complete the fin-whale picture by reference to the findings of Chittleborough (1954). First, it is necessary to show that the size of the fully formed corpus luteum is similar in the two species; it has already been established that the sizes of follicles at different stages of the sexual cycle are similar.

Chittleborough gives a mean diameter for the corpus luteum of 29 females in late pregnancy, when the corpus is at its maximum size, of 12·3 cm. If nine records of early and mid-pregnancy humpback females (Matthews, 1937) are combined with his data the mean diameter is 11·89±1·58 cm. which is virtually the same as the size of the fin-whale corpus luteum, mainly from early and mid-pregnancy (11·44±0·54 cm.). We may, therefore, assume that the details of ovulation in the fin whale, for which we have no direct evidence, are very similar to the condition in the humpback whale.
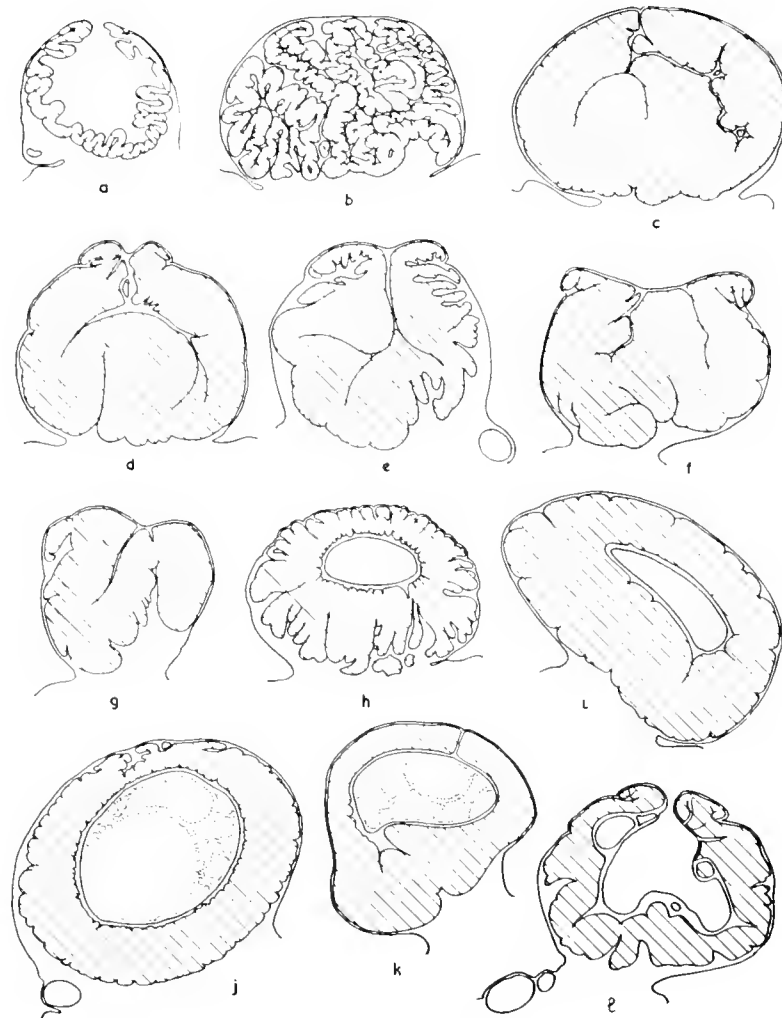
Text-fig. 5. Morphological variation in corpora lutea. See text for explanation.

In the humpback material there were 35 females which were found to have just ovulated, the blood-stained hole (from 4 to 13 mm. in diameter) being immediately obvious on the surface of the ovary. Immediately after ovulation the follicle was collapsed and the wall wrinkled. The size range at this stage was 2·2–6·0 cm. (median 3·7 cm.) and the smallest recently formed corpora lutea are about 4 cm. in diameter (Chittleborough, 1954, fig. 4), suggesting that the size of the original mature follicle at ovulation was of the order of 6–8 cm. (see Harrison, 1948, p. 247). This is in agreement with the maximum size of unruptured mature follicles given by Chittleborough; of five above 6 cm. the mean diameter was 7·1 cm., but four of these lay between 6 and 7 cm. and one was 10·5 cm. in diameter.

In 25 recently ovulated fin whales the largest follicle (which was presumably the second largest at ovulation) had a mean diameter of 3·8±0·53 cm. and the absolute maximum size was 9 cm. Chittleborough (1954, p. 58) gave one example of a female humpback whale approaching ovulation; the two

largest follicles measured 5·3 and 3·7 cm. The fin-whale follicle size at ovulation is probably appreciably greater than 6 cm.

These observations suggest that in the fin whale the follicle ruptures when it enlarges to about 7 cm., possibly at a greater size than this, so that the mature corpus luteum of pregnancy is about one and a half times the size of the follicle at ovulation. Immediately after ovulation the ruptured follicle loses fluid and shrinks to about 4 cm. As the folding of the follicle wall becomes more obvious luteal tissue forms from the granulosa (Text-fig. 5a) and the centre of the ruptured follicle is often filled with a translucent gel, the tertiary liquor folliculi. This central part soon fills with luteal tissue though a central cavity may remain. At the same time the newly formed corpus increases in size.

Harrison (1949, pp. 245–7) has described the histological appearance of a corpus luteum at this stage of development in the pilot whale, *Globicephala melaena*, and concludes that the general appearance is of an open 'lace-like' arrangement of luteinizing granulosa cells. Considerable trabeculation is present (see Text-fig. 5b); projections of theca externa containing thecal vessels form the central core of the trabeculae, and large groups of theca interna cells are present at the bases of the trabeculae and at the periphery of the developing gland. The slit-like central cavity is lined by fibroblasts.

In fin and humpback whales a fresh, unfixed, recently formed corpus luteum can usually be distinguished macroscopically from later stages. The outer membrane is very thin, with numerous blood vessels visible immediately beneath it, and the luteal tissue is soft, pale in colour and expanded in contrast with the firmer, more yellow tissue in later stages and especially during pregnancy. The initial size of the corpus luteum is dependent on the size of the follicle at ovulation. In the recently ovulated class it averages $8·28 \pm 0·82$ cm. (range 1·5–13·5 cm.). Once formed it continues to increase in size for some months if pregnancy supervenes. The distribution of lipoids at different stages of pregnancy is illustrated in plate IV.

BILATERAL ACTIVITY OF THE OVARIES

Slijper (1949) gives records of 17 fin whales for which it was known whether the corpus luteum of pregnancy came from the left or right ovary, and there are 37 similar observations made at South Georgia by the 'Discovery' Investigations. In this sample of 54 fin whales the corpus luteum was in the right ovary in 32 cases (59·2%). Similarly for blue whales, Slijper gives 22 records and there are an additional 21 records from South Georgia. In 24 of these (55·8%) the corpus luteum of pregnancy was in the right ovary. Slijper's original sample indicated that in 59% of blue whales and 65% of fin whales the corpus luteum was in the right ovary.

As regards the distribution of corpora albicantia, there are in all records of 671 corpora albicantia from 69 fin whales and 411 corpora albicantia from 54 blue whales which are relevant. Of these 51·8 and 52·3% were in the right ovary of fin whales and blue whales respectively. Combining both the corpora lutea and corpora albicantia, of 724 fin-whale corpora $52·4 \pm 3·72\%$ were in the right ovary and of 454 blue-whale corpora $52·4 \pm 4·68\%$ were in the right ovary. Even when the blue and fin whale data are combined the distribution is not significantly in favour of the right ovary ($52·4 \pm 2·92$), but nevertheless it seems possible that there is a slight prevalence of the right side in both these species.

Slijper (1949) presents evidence which appears to show that in the Odontocete whales ovulation occurs almost invariably from the left ovary, and he also gives a number of observations which suggest that the left ovary is larger than the right. Both Slijper, and Brambell (1956) refer to the prevalence of the right side in bats, and the left side in monotremes. Slijper suggests that the prevalence of a particular ovary is connected with uniparity and discusses further examples. He presents one case of transference of the ovum from the right ovary to the left uterine cornu in a fin whale.

The corpus luteum of ovulation

There are records of the diameter of the corpus luteum of ovulation of 59 female fin whales. These are in the recently ovulated class of females, taken in the antarctic, the majority outside the usual conception period for the species (see p. 450). They may be characterized as females which had an apparently normally active corpus luteum in the ovaries, but in which an intensive search of the uterus failed to reveal a foetus. Examination of the mean size of the largest follicle in this group (p. 347) confirms this diagnosis.

The size range of these corpora lutea of ovulation is 1·5–13·5 cm. and the mean diameter, 8·28 ± 0·82 cm., is well below the mean size of the corpora lutea of pregnancy (Text-fig. 7). This corresponds to a mean weight of 0·375 kg. and a weight range of 3·4 g. to 1·5 kg. (Text-fig. 8). Some of these corpora lutea of ovulation are of very recent formation (Text-fig. 5b) and show the characteristic unexpanded cross-section of an early stage of formation.

Two of them, which represented first ovulations of females at puberty, were associated with the occurrence of unusual cysts (Text-fig. 6) in the uterine cornu on the same side as the corpus luteum. These cysts were at first thought to be small embryos. They were sectioned by Dr R. Willis (Department of Pathology, The School of Medicine, Leeds), who reported that they do not show any features suggestive of embryonic products or gestational changes. The bulk of the tissue in the walls of the

Text-fig. 6. Vesicles found *in uteri* of two pubertal females.

vesicles is structureless and degenerate, and where surviving tissue is present it seems clear that it must have arisen from the endometrium itself.

In its morphology the corpus luteum of ovulation is similar to the corpus luteum of pregnancy and no constant differences have been observed (see below, p. 362).

The corpus luteum of pregnancy

Size

There are insufficient data from the early stages of pregnancy to justify a precise statement about the duration of the initial phase of growth of the corpus luteum of pregnancy. What there is suggests that the corpus luteum continues to grow until the foetus is about 10–20 cm. in length, at an age of one or two months. It then remains of constant size until late pregnancy. The extensive data now available provide no evidence that the corpus luteum decreases in size towards the end of pregnancy, as Mackintosh and Wheeler (1929) suggested. There is actually some slight indication of an increase in corpus luteum size in late pregnancy, because six corpora associated with foetuses averaging 5·74 m. in length were 5 mm. larger in mean diameter than the mean size in earlier stages of pregnancy. Because of the small size of the sample and the variability in corpus luteum size this difference is not significant.

Chittleborough (1954, p. 46) gives a probable growth curve for the early development of the hump-back-whale corpus luteum by linking the largest corpus luteum found in each month. This suggests that the corpus steadily increases in size for the first two months, when it approaches the range found in late-pregnancy corpora lutea.

The mean diameter of 523 fin-whale corpora lutea of pregnancy was 11·44 ± 0·154 cm. and the

range of variation 6·2–17·5 cm. The lower limit is the smaller of two corpora lutea associated with twin foetuses and the smallest corpus luteum from a uniparous pregnancy is 7·5 cm. The frequency distribution of corpus luteum diameter is shown in Text-fig. 7.

There are 372 records of the weight of fin-whale corpora lutea. The mean weight is 0·881 ± 0·04 kg. and the range 0·2–2·4 kg. The frequency distribution is shown in Text-fig. 7. Chittleborough (1954) suggests that there is a relation between the weight of the corpus luteum and the age of the female
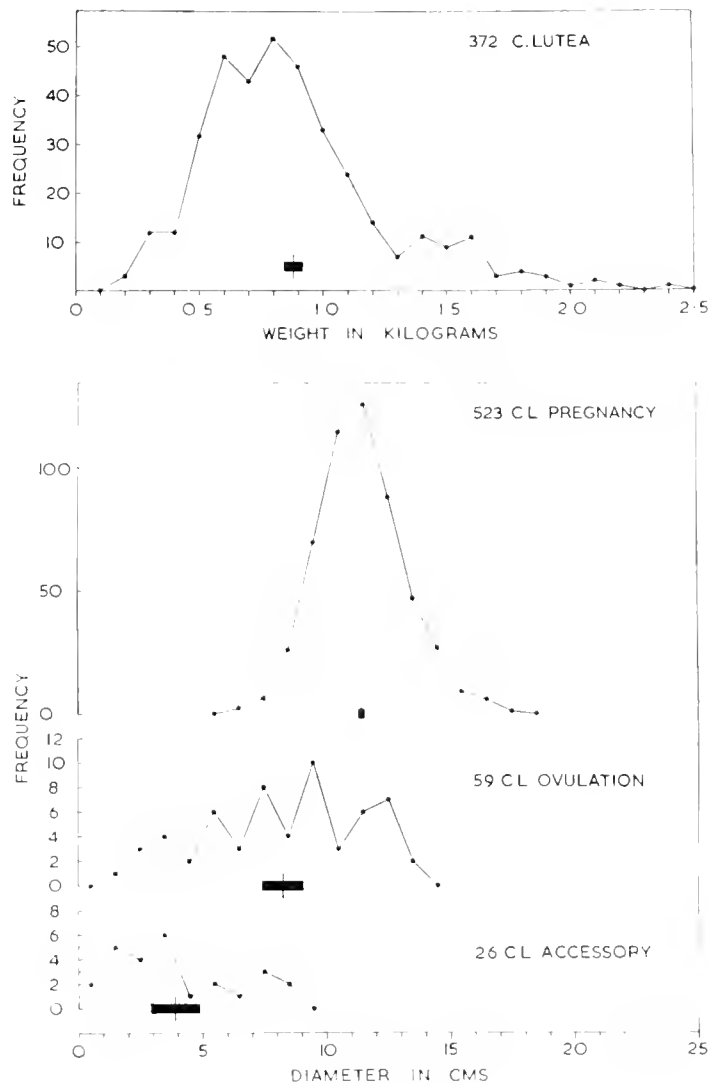
Text-fig. 7. Frequency distributions of weights and diameters of corpora lutea.
The means ± 2 S.E. are shown.

using the total number of corpora in the ovaries as an index of relative age. He found an increase in corpus luteum size with increasing age. In fin whales no such increase in size could be demonstrated.

In Text-fig. 8 average corpora lutea weights at different diameters have been plotted on a double logarithmic scale for 372 fin whales. Five blue-whale records and three sperm-whale records have been added at the upper and lower limits of the size range. This gives a linear relationship, as is to be expected, and suggests a probable maximum weight for the extreme fin-whale corpus luteum diameter (17·5 cm.) of 3·2 kg. Thus the extreme weight range in this larger sample is from 0·14 to 3·2 kg., a sixteen-fold increase from smallest to largest, as compared with a less than three-fold increase in diameter (6·2–17·5 cm.).

In further discussions of the size of the corpora lutea and corpora albicantia the mean diameter will be used as a measure of size instead of weight both because of its smaller variability and because there are many more records of diameter than of weight. This applies especially to the corpora albicantia which, being usually embedded in the ovary, are difficult to weigh accurately.

Morphology

The various morphological types of corpora lutea are illustrated in Text-fig. 5 and Pl. IV, fig. 1. The corpus almost invariably protrudes from the surface of the ovary and is sometimes connected only by a narrow neck of tissue (as in Text-fig. 5 k, l). This is probably related to the relatively rigid fibrous structure of the stroma, for in the smaller sperm-whale and pilot-whale ovaries, which are less fibrous, the corpora lutea do not usually protrude so much. The overall shape of the corpus is spheroidal and some are flattened, with an oval cross-section. The point of rupture of the original follicle is usually visible as a small stigma, surrounded by a corona of everted pinkish-yellow tissue, which is usually about 2–4 cm. in diameter. In sections the luteal tissue is seen to be tortuously folded and tightly packed, as if Text-fig. 5 b had been tightly compressed. This meandrine appearance is due to the initial folding of the follicle wall and the growth of fibrous trabeculae, which carry the blood vessels supplying the gland. The central cavity is compressed at an early stage to a thin slit. The fibrin in this slit is replaced by connective tissue so that septa ramify throughout the gland in a pattern complementary to the trabeculae formed by ingrowth of the theca externa. These internal connective tissue septa have no blood vessels Pl. IV, fig. 2.

Text-fig. 8. Relation of weight to diameter for whale corpora lutea and corpora albicantia (fin whale mean values; other species, single records).

The most commonly formed corpora lutea are types c, d and e in Text-fig. 5. Together they constitute 70% of a sample of 88 fin-whale corpora in which the morphology was noted. Types d and e are the most common, comprising 48% and type c, in which there is a stigma but no corona, comprises 22%. The next most abundant type are corpora lutea in which the central cavity has not been completely obliterated after ovulation (types h–k). In this small sample 17% were of this type. In a larger sample of 107 vesicular corpora lutea the cavity varies in size from 3 mm. to 13·3 cm. in diameter. The larger corpora lutea have the larger vesicles, the mean cavity diameter increasing from 1·8 cm. at a corpus diameter of 7–8 cm. to 4·1 cm. at a corpus diameter of 14–15 cm. (Text-fig. 9). The cavity is filled with gel, fluid, or fibrin strands and bounded by a thick layer of avascular hyaline connective tissue.

Another type is the everted corpus luteum. In these corpora the corona may be equal to (Text-fig. 5 f) or greater than (Text-fig. 5 g) the mean diameter of the corpus luteum. The largest corona measured was 12·3 cm. in diameter (from a corpus luteum 13·3 cm. in diameter) and the second largest was 10·5 cm. across. The first, partially everted, type accounts for 8% of this sample and the fully everted type for 3%. The least common type is very similar to the cavitate bodies, but the stigma is widely open, there is no gel or fluid and the hyaline inner wall is usually very thick (Text-fig. 5 l). Only 2% (two cases) of the corpora in this sample were of this type, and the true percentage in a larger sample would be very small because if observed in the course of routine slicing this shape has invariably been noted.

Vesicular corpora lutea

In Text-fig. 5, these morphological types have been arranged in the order of their development. They fall into two main groups; the non-vesicular types (*c–g*) which are obviously related, and the corpora with cavities (types *h–l*). In a large sample of 701 corpora lutea which were grouped according to the presence or absence of a cavity 17·1 % had a cavity. Often the vesicular type lack a corona and the stigma is inconspicuous. In the single specimen of type *k*, the thinner part of the wall gave the impression that it had been under pressure from the liquor folliculi. The connective tissue septa are radially arranged in a regular pattern. This radial arrangement of trabeculae and internal septa is observed in all the corpora with large vesicles, but not in type *l*.

The mode of formation of the cavity calls for some comment since Dempsey and Wislocki (1941) and Robins (1954) have suggested that cavity formation in the humpback whale is related to the large size of the corpus luteum. Robins suggested that the absence of a cavity is diagnostic of a corpus luteum of ovulation and this, if true, would be of great value in studies on the reproductive cycle and of age-determination.

Dempsey and Wislocki base their conclusions on the examination of 16 pairs of ovaries, not all of which were from pregnant females. The corpora lutea they examined were 3–6 cm. in diameter so, even allowing for excessive shrinkage as a result of fixation (which is not borne out by the histological appearance), they are well below the normal size range for corpora lutea of pregnancy in both fin and humpback whales. In fact it appears likely that they were corpora lutea of ovulation. These authors 'conclude that the large size of the whale's corpus luteum imposes certain anatomical peculiarities and physiological limitations on its vascular supply. The luteal arterioles and capillaries are apparently unusually long. The functional restrictions in consequence of the lengthening of these vessels make it impossible for the luteal tissue ever to fill the entire cavity of the luteal body. These limitations result also in nearly complete avascularity of the centre of the corpus luteum, associated with excessive fibrosis and hyalinization' (p. 250).

Robins (1954) found that in all the functional corpora lutea (37 in number) which he examined from both early and late pregnancy there was a central cavity, 'variable in size but always quite noticeable'. He also found that a variable proportion of corpora lutea [corpora albicantia?] did not possess this characteristic cavity or core. Robins suggested that, owing to the small size of the corpus luteum of ovulation (up to 88 mm.) there appears to be no anatomical limitation on the blood supply and luteal cells continue to fill the cavity so that no distinctive centre remains. This is supported by several whales which had ovulated twice without successful fertilization and showed the regressing corpora lutea to lack the characteristic centre of the corpus luteum of pregnancy. According to Robins, if pregnancy intervenes the gland continues to expand and, in accordance with the ideas of Dempsey and Wislocki, anatomical limitations prevent blood vessels from supplying the centre of the gland so that a thick avascular hyaline zone forms, limiting the thickness of the luteal tissue and causing the central cavity to be retained.

There are several important objections to this hypothesis. It has been pointed out that the corpora examined by Dempsey and Wislocki were only 3–6 cm. in diameter, but nevertheless contained central cavities. The corpus luteum of ovulation is of this order of size. Personal examination of humpback-whale ovaries from the Antarctic (unpublished) shows that the non-vesicular corpora lutea of pregnancy are more common than the type with cavities. Chittleborough (1954) illustrates a 12-cm. functional corpus luteum of late pregnancy which clearly has no central cavity.

It has been established that in the fin whale only 17·1 % of the corpora lutea have a cavity. Corpora lutea are found up to 16 cm. in diameter which are without cavities and a blue-whale corpus luteum

of pregnancy which was 19 cm. in diameter lacked a cavity. Conversely, cavities are found in the much smaller corpora lutea of other animals; in man, for instance, corpora lutea of pregnancy or ovulation less than 1 cm. in diameter commonly have cavities (Dubreuil and Rivière, 1947) and vesicular corpora lutea are relatively common in the cow (Hammond, 1927). These observations mean that the hypothesis of vascular limitation is untenable.

Secretion of fluid by the follicle wall continues for an appreciable time after ovulation and vesicular corpora lutea in other mammals are usually attributed to the continued secretion of liquor folliculi by the ruptured follicle after the aperture has become closed (Brambell, 1956, p. 474). According to Robinson (1918) the persistence of the central cavity in the ferret depends on the degree of separation of the internal limiting membrane at ovulation. The point of rupture of the follicle is closed by a tenacious coagulum, the tertiary liquor folliculi, which also redistends the collapsed follicle often to the size it originally was before ovulation (Harrison, 1948).
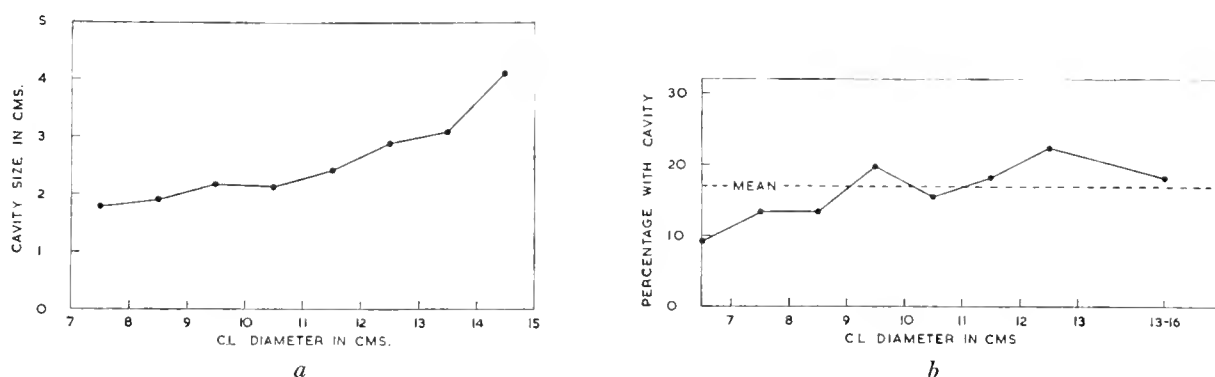
Text-fig. 9. *a*, Relation between cavity diameter and corpus luteum diameter. *b*, Relation between corpus luteum size and the incidence of cavities.

The appearance of fin-whale corpora lutea of the vesicular type suggests that they are usually formed in this way. In most corpora with large cavities (Text-fig. 5*h*–*k*) the stigma is inconspicuous and there is no eversion of luteal tissue to form a corona. This suggests that the aperture became closed again after ovulation and remained closed. The corpus illustrated in Text-fig. 5*k* has a small stigma, but the corpus has a distended appearance and the luteal tissue has obviously been subjected to pressure from inside, presumably by continued secretion of fluid. The most uncommon type of corpus (Text-fig. 5*l*) has an opening and a conspicuous corona. It immediately suggests that the aperture closed after ovulation, but that the internal fluid pressure later forced it open when the corpus luteum had almost attained its definitive size and form.

There is a relation between the size of the corpus and the size of its cavity (Text-fig. 9*a*). For 107 fin-whale corpora for which the cavity size is known the mean size of the cavity increases from 1·8 cm. at a corpus size of 7–8 cm., to 4·1 cm. at a corpus size of 14–15 cm.

There is also a relationship between the size of the corpus luteum and the prevalence of the vesicular type. For 701 corpora lutea, 120 of which have cavities, the percentage of vesicular corpora in successive size groups increases from about 10% at a corpus size of 6–7 cm. to about 20% in corpora above 13 cm. in diameter (Text-fig. 9*b*). In other words the larger corpora show a greater tendency to have cavities. Extrapolation suggests that corpora below 3–4 cm., forming from ruptured follicles, would not be vesicular. The limited material available supports this. In Text-fig.10 a number of small accessory corpora lutea are illustrated and all which have central cavities are formed from unruptured follicles. These accessory corpora lutea are produced in such limited numbers that they do not affect the figure for the percentage of corpora with cavities. Corpora lutea of ovulation with a mean diameter

of $8\cdot28\pm0\cdot82$ cm. might be expected to include a slightly lower proportion with cavities than pregnancy corpora. Of fifteen corpora lutea of ovulation examined in 1953/54 and 1955/56, only one (6·7%) possessed a central cavity, but this is too small a sample to give a significant result.

ACCESSORY CORPORA LUTEA

Of 760 corpora lutea examined, 28 or 3·7% were accessory corpora ranging from 0·4 to 8·5 cm. in diameter, the mean diameter being $3\cdot88\pm0\cdot8$ cm. and the weight about 45 g. It is likely that many more small accessory corpora lutea form, but corpora less than 7 mm. in diameter are usually missed in the routine examinations; one accessory corpus 1 mm. in diameter has, however, been seen in histological preparations. The material is rather too sparse to allow firm conclusions to be drawn, but accessory corpora lutea of ovulation appear to occur as frequently as accessory corpora lutea of pregnancy.
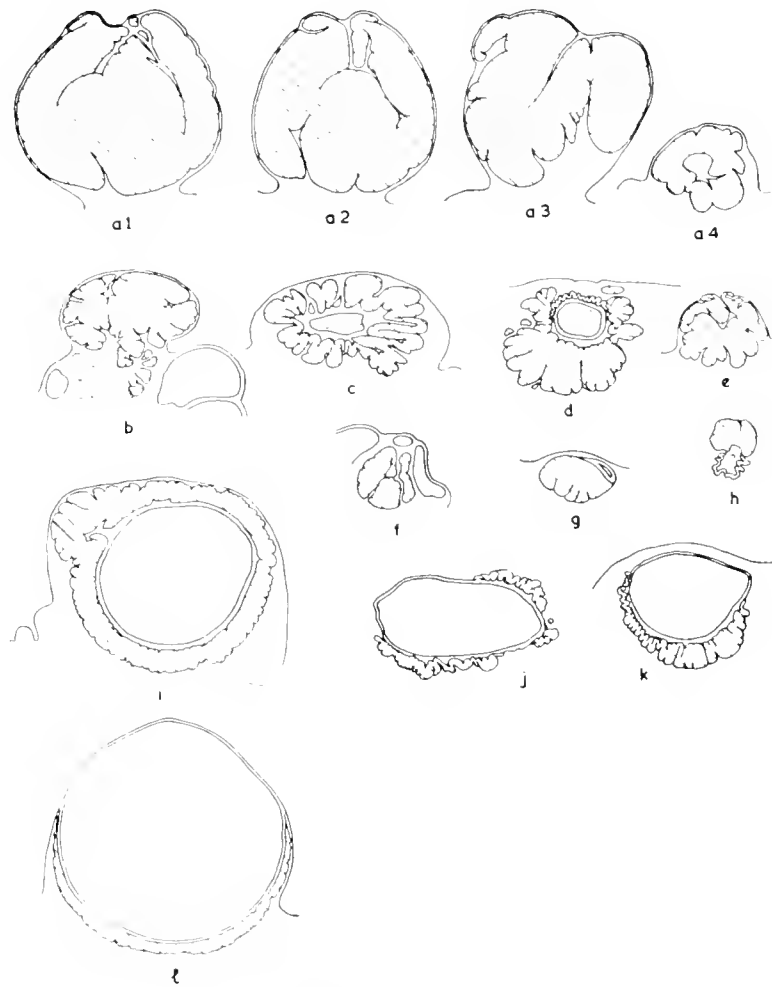
Text-fig. 10. Morphological variation in accessory corpora lutea. See text.

They fall into two main groups; the larger, having developed from ruptured follicles, show a stigma and small corona, but the smaller are formed from unruptured follicles.

A female fin whale 73 ft. in length taken on 8 February 1954 had recently ovulated, but no products of conception were seen in the uterus. There were three small corpora lutea in one ovary, one of which, 23·5 mm. in diameter, had ovulated, and two measuring 13 and 15 mm. (Text-fig. 10 g, h) had developed from unruptured follicles. The appearance of the luteal cells is similar in all three. They are derived from the membrana granulosa because theca interna cells can be seen at the periphery of the gland

and at the base of the trabeculae. Only part of the follicle wall has contributed to the luteal tissue and for the most part the follicle has undergone avascular hyaline degeneration to form a hard knob of collagenous tissue.

Other accessory corpora illustrated in Text-fig. 10, have formed in this way either from the whole (c, i) or part (d, g, h, j, k, l) of the mural epithelium. Quite large accessory corpora can form without ovulation; one measuring 37 mm. in diameter is illustrated in Text-fig. 10 a 4. This was the smallest of four active corpora in the ovaries of a 76-ft. female taken on 27 February 1954, which was pregnant with a 4·2 m. male foetus. There were 11 corpora albicantia. The three largest corpora lutea have formed from ovulated follicles and one is conspicuously everted, with a corona measuring 7·5 × 8·0 cm. Another accessory corpus luteum (Text-fig. 10b) which measures 4·5 cm. has a stigma on the surface of the ovary and one lobe of luteal tissue is undergoing hyaline regression. Text-fig. 10 f is an example of an accessory corpus luteum, 1·9 cm. in diameter, formed from an unruptured follicle, in which the central cavity has been obliterated by an ingrowth of luteal tissue.

These small accessory corpora formed from unruptured follicles are similar to the 'corpora lutea atretica' of Brambell (1956, p. 501), but the membrana granulosa appears not to degenerate and theca interna cells are distinguishable at the periphery.

CONCLUSIONS

In fin whales there is perhaps a slight tendency for the right ovary to ovulate more frequently than the left ovary. It appears that the size of the mature graafian follicle of fin whales at ovulation is about 7 cm. but there is clearly a great individual variation in size at this stage.

The corpus luteum of ovulation averages 8·28 cm. in diameter, weighs about 375 g. and probably persists for 15–20 days. There is no evidence that pseudopregnancy ever occurs. If pregnancy supervenes, the newly formed corpus luteum continues to grow for about 2 months, when it reaches an average size of 11·44 cm. and weighs about 881 g. There is no evidence of a decrease in size in late pregnancy. No correlation between the size of the corpus luteum and the age of the female has been found. Accessory corpora lutea of ovulation or pregnancy are uncommon, those above about 7 mm. in diameter amounting to only 3·7% of all corpora lutea. They form either from ovulated follicles or by luteinization of smaller unruptured follicles, and have a mean diameter of 3·88 cm. and an average weight of about 45 g. Additional corpora lutea are not formed during pregnancy.

No constant morphological or histological differences have been found between corpora lutea of ovulation and corpora lutea of pregnancy. The incidence of vesicular corpora has been studied and gives no support to Robins's (1954) suggestion that the presence or absence of a cavity is diagnostic of a corpus luteum of pregnancy or a corpus luteum of ovulation respectively. In fact only 17·1% of corpora lutea of pregnancy have a fluid- or gel-filled cavity. Nor does the material support the contention of Dempsey and Wislocki (1941) that the factor responsible for the formation of a cavity is a restricted blood supply to the centre of the large corpus luteum of the whale. A corpus luteum 19 cm. in diameter possessed no central cavity. There is, however, some evidence that the larger corpora lutea show more of a tendency to be vesicular than the smaller corpora, but the difference is only 10% over the size range 6–13 cm. It appears that at corpus sizes below about 3–4 cm. a cavity is present only in some of those accessory corpora which have developed from unruptured follicles.

The presence or absence of a cavity or, in corpora albicantia, of a central core of connective tissue, cannot, therefore, be used to distinguish the corpora formed as a result of ovulation only, from those representing pregnancy (see also p. 365).

Van Lennep (1950) suggests that at the same stage of regression corpora lutea of ovulation can be expected to be smaller than corpora lutea of pregnancy and this might afford a means of distinguishing

between corpora albicantia of ovulation and pregnancy. The total size range of corpora lutea of ovulation and pregnancy is 16·0 cm. and the overlap is 7·3 cm., so size alone cannot be diagnostic. It is suggested below that size correlated with a quantitative measurement of histological regression could perhaps be used to distinguish these two types of corpora in individual females.

Van Lennep also suggests that two types of corpora albicantia can be distinguished, those with straight connective tissue trabeculae and those with branched trabeculae. He suggested that 'Most, if not all, corpora albicantia of the first type are probably derived from corpora lutea of ovulation as only young corpora lutea of pregnancy have been found to possess the same structure and may therefore be supposed to become corpora albicantia of the second (branched) type' (p. 597). It is shown later that these types of corpora albicantia correspond to vesicular and non-vesicular corpora lutea respectively. In fact van Lennep's distinction is the reverse of that suggested by Robins. Finally, mention must be made of the comprehensive paper of Dubreuil and Rivière (1947), who conclude that there is still no certain means of distinguishing the human corpora lutea of pregnancy and ovulation. Much attention has been given to this subject because of the legal implications. The work of Peters bearing on this problem will be discussed in the next section (p. 384).

CORPORA ALBICANTIA, CORPORA ABERRANTIA AND CORPORA ATRETICA

The corpus albicans

The corpus luteum of ovulation after 2–3 weeks and the corpus luteum of pregnancy after about 11 months undergo degenerative changes and rapidly shrink in size. The luteal cells disappear, the colour of the former lobes of luteal tissue changes to a tawny brown and the white connective tissue septa become increasingly more conspicuous (Pl. V, fig. 1).

There is some confusion about the nomenclature of the body so formed. The regressed corpus luteum of the whale is not properly a corpus albicans, a term which is correctly applied to the unpigmented old corpora of certain other animals. Usually some pigment remains even in the very old corpus of the fin whale and the more recent regressing bodies are well pigmented like the corpus rubrum of the cow, although they are a yellow-brown in colour. The term corpus fibrosum might be applied to the old corpus which has lost most of its pigment.

Mackintosh and Wheeler (1929) refer to the active corpora lutea and the regressed corpora lutea as corpora lutea *a* and *b* respectively. The latter is technically a more correct terminology than corpus albicans, but it leads to confusion. The term corpus albicans is now generally used to describe old corpora lutea whether pigmented or not, and to avoid introducing yet another terminology it is proposed to refer to all old corpora lutea as corpora albicantia.

The corpus albicans material is much more extensive than that available for study of the corpus luteum, because one pair of ovaries may contain over fifty corpora albicantia, but usually only one corpus luteum. In 1953/54 a detailed study of 1381 fresh unfixed corpora albicantia was undertaken by the author in F/F 'Balaena', and various morphological types were distinguished. These ovaries were sliced by hand. Unfortunately no large collection of fin-whale ovaries was undertaken in 1954/55, and it was not until after the 1955/56 season that a collection of ovaries became available for routine examination. Using a slicing machine cutting at 5 mm., all the corpora above about 7 mm. were examined and some of those smaller than this. In all 4065 corpora albicantia were systematically examined, classified and measured. It is necessary to make clear one important point about the measurements. In calculating the mean diameter of the corpus luteum, measurements were made on three axes. Since most corpora albicantia are embedded in the ovary and do not project like the

corpus luteum, routine measurements of only two diameters have been practicable during slicing. It is assumed that since the corpora appear to be randomly oriented, this does not introduce any important degree of error into the results. The corpora were placed in three morphological classes (independent of size) to be described below. These are termed 'young', 'medium' and 'old' corpora albicantia, and are believed to represent three definite stages in the regression of the corpus luteum. The evidence for this view is presented below.

The mean diameter of 3181 corpora albicantia from pregnant females is $2 \cdot 56 \pm 0 \cdot 03$ cm., and for 884 from non-pregnant females it is $2 \cdot 52 \pm 0 \cdot 07$ cm. From this season there are only 89 corpora albicantia from females known to be lactating, and the mean size is $2 \cdot 5 \pm 0 \cdot 9$ cm. These differences are not significant, and this mean diameter corresponds to a weight of about 10 g. (see Text-fig. 8). In Text-fig. 11 the percentage size frequency distribution of these corpora albicantia from pregnant
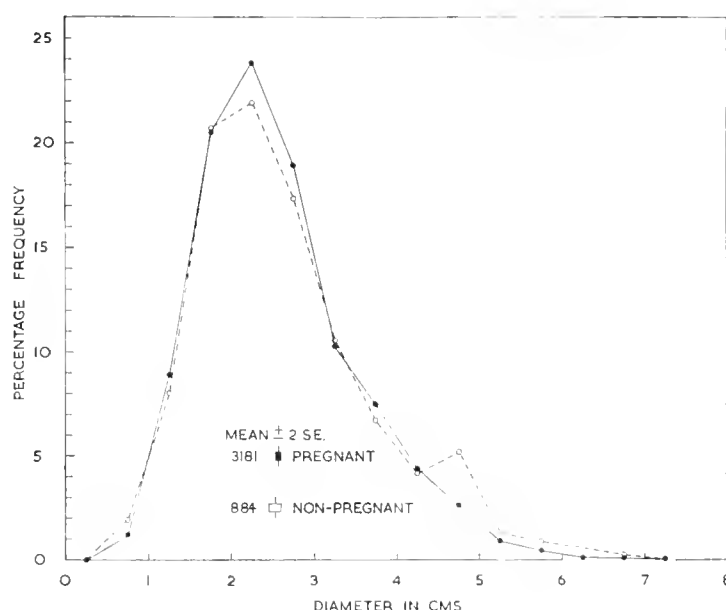
Text-fig. 11. Frequency distributions of corpora albicantia sizes. ●——● pregnant; ○– – –○ non-pregnant.

and non-pregnant females is presented. They range in size from 7 to 80 mm. corresponding to a variation in weight from less than 0·4 g. to about 300 g. It will be noticed that a proportion of non-pregnant females ('resting females') have a large corpus albicans about 4·75 cm. in diameter, whereas the curve for pregnant females lacks this subsidiary peak. The modal diameter for both groups is 2·25 cm. Only 34 corpora albicantia have been weighed, mostly in the size range 4–7 cm., because it is difficult to isolate corpora albicantia for weighing, embedded as they are in the ovarian stroma. The results have been incorporated in Text-fig. 8 where the mean weights for corpora albicantia 2–3 cm., 3–4 cm., 4–5 cm., etc. in diameter are plotted on a double logarithmic graph. These points fall along the regression line for corpora lutea, so there has been no observable alteration in density corresponding to the change from corpus luteum to corpus albicans. Corpora albicantia sizes will be discussed more fully when the different morphological classes have been described.

Morphological types

In Text-fig. 12 and Pl. V, fig. 1 the various morphological types of corpora albicantia are illustrated and if they are compared with the corpora lutea illustrated in Text-figs. 5 and 10 the similarity in their architecture is readily apparent. In general the white connective tissue septa of the corpus albicans are much thicker than those in the corpus luteum and the lobes of brown hyaline collagen, representing the

transformed luteal tissue, occupy relatively less space. All stages in regression are seen, from bodies similar to the corpus luteum, to bodies in which the connective tissue septa have enlarged at the expense of the pigmented tissue so as to fill almost the whole volume of the corpus (Pl. VI, fig. 1). One macroscopically visible feature which enables even the most recent corpora albicantia to be distinguished from the corpus luteum is the relatively sudden change in the appearance of the luteal tissue from an opaque yellow, to a hyaline brownish yellow. Occasionally a corpus luteum is found in which some lobes are hyaline, others still characteristically luteal and others intermediate in condition.
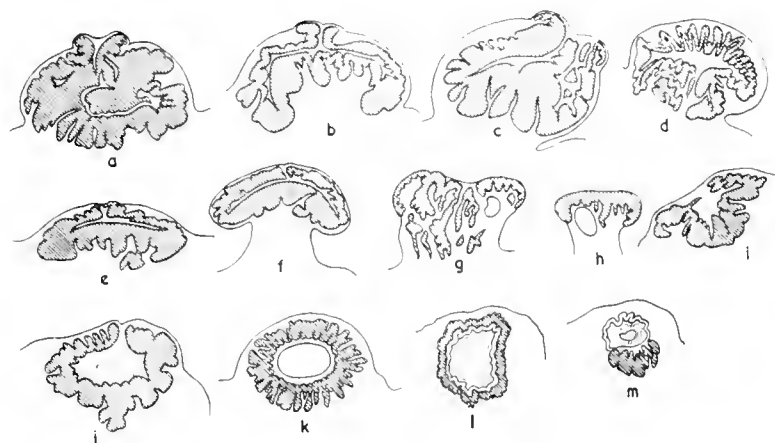
Text-fig. 12. Morphological variation in 'young' and 'medium' corpora albicantia.

Table 3. *Incidence of vesicular or radiate corpora in different groups*

	Total	No.	Percentage	2 S.E.
		With cavity		
All corpora lutea pregnancy	701	120	17·1	2·88
All corpora albicantia	1381	246	17·8	2·05
All corpora lutea + all corpora albicantia	2082	366	17·6	1·66
'Young' + 'medium' corpora albicantia	484	88	18·2	3·40
'Old' corpora albicantia	897	158	17·4	2·54
All corpora albicantia associated with a vesicular corpus luteum	231	47	20·4	5·01

The most distinctive bodies are the corpora albicantia with a central cavity or core of connective tissue, and a stellate structure with septa arranged radially (Text-fig. 12k and Pl. VI, fig. 3). These clearly represent the products of regression of vesicular corpora lutea and a consideration of their frequency is confirmatory. If the corpora lutea and corpora albicantia samples are combined there is a sample of 2082 corpora and the incidence of the vesicular type is $17·58 \pm 1·66\%$. The percentages of this type among 'young' and 'medium' and 'old' corpora albicantia (as defined below) are given in Table 3, which shows that the differences are not significant. It appeared likely that in ovaries where the corpus luteum was of the vesicular type there was a higher proportion of 'radiate' corpora albicantia ($20·35\%$) suggesting that some females had more tendency than others to accumulate this type of corpora, but this difference in the percentages is found to be not significant.

We may conclude that the incidence of the vesicular type of corpora does not vary significantly among different groups of corpora albicantia and corpora lutea. This also confirms that the incidence of cavities is not appreciably different in corpora lutea of ovulation compared with corpora lutea of pregnancy. Since the production of corpora of ovulation presumably equals or outnumbers the

production of pregnancy corpora lutea in the life of the whale, if there were any important difference such as Robins (1954) or Van Lennep (1950) suggest, this would affect the proportion of 'radiate' corpora albicantia and it might be expected to be significantly higher (Van Lennep) or lower (Robins) than the incidence of vesicular corpora lutea of pregnancy.

Age groups of normal corpora albicantia

Three groups of corpora albicantia have been identified in fin-whale ovaries on the basis of gross anatomical and histological changes. Since they have an important bearing on age determination in whales they must now be described in some detail. The corpora have been examined macroscopically,
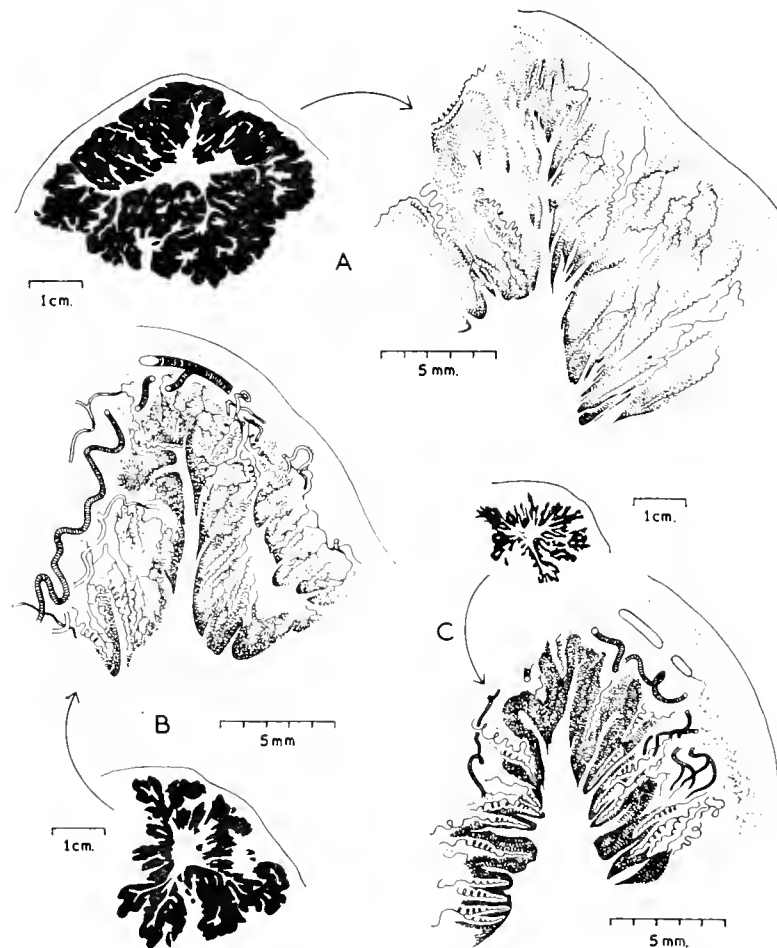
Text-fig. 13. A, typical 'young' corpus albicans; B, typical 'medium' corpus albicans; C, 'old' corpus albicans which still has a conspicuous pigmented layer. (Large-scale drawings are from thick sections cleared in xylol and methyl salicylate.)

when fresh or after fixation in formalin; by examination of 5 mm. thick slices cleared in xylol and methyl salicylate; and by histological examination of material fixed by various techniques. The material for histological examination has been fixed in formalin, Bouin's fluid, and Zenker-formol (Helly) and part of the latter material was post-osmicated with 2% osmium tetroxide to demonstrate the distribution of lipoids. This material has been embedded and sectioned by the standard paraffin wax technique and stained with Heidenhain's Iron Haematoxylin and Eosin, Delafield's Haematoxylin and Eosin, Mallory's trichrome, Masson's trichrome, and Van Gieson.

The routine macroscopic examinations and counts are made by eye on formalin-fixed material.

'Young corpora'

This group includes those corpora which have undergone least regression; some are very recent bodies, parts of which still appear macroscopically like the corpora lutea from which they have developed.

The size range of 628 corpora of this type is 1·5–7·5 cm., mean diameter 4·01 ±0·07 cm., corresponding to a weight of about 41 g. The great range means that size cannot be used as a distinguishing character. Usually, but not invariably, corpora of this type project from the surface of the ovary after the fashion of corpora lutea.

The macroscopic appearance of a typical 'young' corpus albicans is shown in Text-fig. 13 A and Pl. V, fig. 1. There is a conspicuous central core of white connective tissue, but the lobes of brown collagenous tissue are extensive and the connective tissue septa are rather inconspicuous. It appears that when the corpus luteum regresses the blood supply to the luteal tissue is cut off and hyaline degeneration of this tissue then occurs. As the luteal cells are replaced the corpus luteum shrinks in size and the network of connective tissue strands condenses and becomes more conspicuous.

In the 'young' corpus albicans, vascular reinvasion of the pigmented collagenous tissue has begun, and a number of spiral arteries can be seen, but it has not progressed very far (Text-fig. 13 A and Pl. V, fig. 2). The white connective tissue core and septa, representing the original cavity of the newly ruptured follicle, are avascular and remain so throughout subsequent regression.

Examination of cleared thick sections shows the yellow pigment granules to be distributed evenly throughout the hyaline collagen. Sometimes, in very recent corpora, they are very densely arranged so as to give the corpus a shining golden-yellow appearance. Thin sections stained for lipoids (Zenker-formol fixed, and post-osmicated) show the distribution of pigment very clearly (Pl. V, figs. 2, 3, 5, 6).

Rossman (1942) has shown that the pigments of the corpus luteum and the corpus albicans have little in common. He states that it is generally held that the colour of the corpus luteum is due to a carotenoid dissolved in lipin droplets (see Pl. VI, figs. 3–5) so that the colour largely disappears on treatment with fat solvents. The pigment of whale corpora albicantia does not dissolve in fat solvents (xylol, methyl salicylate), which suggests that it is similar to the 'luteolipin' described by Rossman in the corpora of the rhesus monkey, *Macaca rhesus*.

'Medium' corpora

These represent a later stage of regression and have usually sunk into the general stroma of the ovarian cortex so that they do not project very far. They retain a characteristic stigma and corona at the surface. They are smaller than the more recent corpora with a mean diameter, for a sample of 1098 of 2·94 ±0·045 cm., corresponding to a weight of about 15 g. The size ranges from 0·7 to 5·5 cm. and this character is not used for identification.

The macroscopic appearance of a typical 'medium' corpus albicans is shown in Text-fig. 13 B. The central white connective tissue core does not show further enlargement from the 'young' condition, but as the corpus shrinks in volume the septa become rather more conspicuous. The most characteristic macroscopic change is a reduction in the amount of brown hyaline tissue. In thick cleared sections vascularization can be seen to have progressed much further, and there are large thick-walled vessels at the periphery of the corpus. This tangle of sclerotic blood vessels gives to the corpus a thick white connective tissue capsule. Material stained for lipoids shows that there is a clear unpigmented zone of collagen in the vicinity of the blood vessels (Pl. V, fig. 2), and demonstrates that phagocytic activity proceeds inwards from the vascularized outer trabeculae towards the inner avascular connective tissue septa. As the phagocytes take up the pigment and move inwards they concentrate the

pigment so that the colour of the lobes darkens with age. This progressive invasion by blood vessels and phagocytes is shown in Text-figs. 13 A, B, and C, Text-fig. 14 and in Pls. V–VII.

In the 'medium' corpora the smaller spiral vessels are more numerous in comparison with the 'young' corpus, and often impart a reddish hue to the pigmented layer so that bodies of this group are usually a darker reddish brown in colour as opposed to the tawny brown, or even yellow colour of the most recent corpora albicantia.

'Old' corpora

Evidence shortly to be presented establishes that this group represents the final stages of regression of whale corpora lutea, and within this group there is no further reduction in size. The mean diameter of 2339 'old' corpora albicantia is $2 \cdot 013 \pm 0 \cdot 025$ cm., corresponding to a weight of about 5 g., and the size range is from $0 \cdot 7$ to $5 \cdot 0$ cm.

They are characterized by increased centripetal penetration of thick-walled blood vessels and closing of the lumen of vessels near the periphery so that the external white connective tissue trabeculae become even more conspicuous. The layer of pigmented tissue is further reduced and concentrated so that it forms a thin hyaline pigmented zone separating the inner, avascular, connective tissue from the outer trabeculae which are now much thicker and composed largely of contorted non-functional thick-walled blood vessels (Pl. VII, fig. 1). Text-fig. 13 C shows the macroscopic appearance of one of the least regressed corpora in this group, which still has a conspicuous amount of pigmented hyaline tissue. Text-fig. 13 C, Text-fig. 14 and Pls. V–VII show how the pigmented tissue is replaced by blood vessels growing centripetally.

I mm.

Text-fig. 14. Thick cleared section of a typical 'old' corpus albicans. Note avascular core and internal septa below.

There is no further reduction in the volume of the corpus albicans which is now composed largely of unpigmented collagen, and further regression takes the form of progressive vascular and phagocytic invasion and continuing reduction of the area of the pigmented zone. As this becomes thinner it becomes increasingly more densely pigmented and the final stages of regression which have been observed show in section an almost white, avascular, connective tissue body with a very thin darkly pigmented zone outlining the internal septa. In places this pigmented zone may be completely resorbed, as in Pl. VI, figs. 4–7. The reduction and concentration of the pigmented area and its replacement by sclerotic arteries is illustrated in Pls. V and VI.

The rate of thickening of the walls of the blood vessels during regression of the corpus albicans is shown in Text-fig. 15. For each of 10 'old', 12 'young' and 'medium' corpora albicantia and one corpus luteum measurements of the external and internal diameters of the arterioles were made with a projection microscope. Only data from stained sections of corpora in which it was possible to measure 10–20 independent arterioles have been used, which explains the small size of the sample. The mean percentage thicknesses of the vessel walls for the three groups of corpora are plotted against the mean corpus diameter in centimetres, and it appears that the rate of the regression in size of the corpora albicantia is correlated with the rate of change in the thickness of the vessel walls. Once the corpora enter the 'old' group their volume does not decrease further, but it is likely that the vessels

finally lose their lumen and become solid cords of connective tissue. There is some evidence that the external diameter of the arterioles may also increase with age. The average diameter of 10 arterioles in the single corpus luteum examined is 95·3 μ, for 147 arterioles from 'young' and 'medium' albicantia it is 109 μ, and for 111 arterioles from 'old' corpora it is 130 μ. This difference is not, however, statistically significant.

The relative thickness of the vessel wall seems to be a better quantitative index of the age of the corpus than the diameter of the corpus and in general there appears to be less overlap between the two groups of corpora albicantia in respect of this character. It would be interesting, though laborious, to determine the relative thickness of the arteriole walls for a complete series of say thirty corpora albicantia from one pair of ovaries so as to gain some idea of the variation in corpus size within a single animal. Since for corpora albicantia of similar age, those formed from corpora lutea of ovulation will be smaller than corpora albicantia of pregnancy, it might perhaps be possible to identify corpora of these two origins and to place them in a chronological series. It might also be possible in this way to establish the relative frequency of corpora lutea of pregnancy and ovulation. This is the only possible means of distinguishing corpora albicantia of pregnancy from corpora of ovulation which is suggested by the present study. It depends on the assumption that although there is a large variation in corpus luteum size in the whole population, for a single female it might be expected that the size variation in corpora lutea of these two origins would be slight.

Text-fig. 15. Relation between size of corpus and thickness of arteriole walls (corpus luteum—triangle; 'young' and 'medium' corpora albicantia—open circles, 'old' corpora albicantia—black circles).

Persistence of corpora albicantia

In the routine examination of the 1955/56 ovary collection 4065 corpora albicantia were classified into these three stages of regression—'young', 'medium' and 'old'—on the basis of their macroscopic appearance in the 5 mm. slices. The main criteria used are the relative amounts of white connective tissue and brown 'luteal' tissue. These types represent stages in a continuous process so there is no definite line of demarcation between corpora in each of the groups and it is sometimes difficult to decide in which of two groups a corpus should be placed. This applies more to distinguishing 'young' from 'medium' corpora than 'medium' from 'old'. In a large sample these marginal corpora may be expected to cancel each other out. In addition to the author, two colleagues (Mr A. E. Fisher and Mr J. H. Smoughton) have independently undertaken the examination of parts of the material, and the fact that the results are consistent although obtained by three separate workers supports the validity of the classification.

In Text-fig. 16 the frequency distribution of mean diameters of these three types is presented. There is an extensive overlap between all three groups; the size range for 'young' corpora is 1·5–7·5 cm., for 'medium' corpora 0·7–5·5 cm., and for 'old' corpora 0·7–5·0 cm. The mean values and two standard errors are 4·01 ± 0·07, 2·94 ± 0·05 and 2·01 ± 0·03 cm., respectively. The frequency distribution for each group is as symmetrical as for the corpus luteum size frequency (Text-fig. 7). The youngest corpora albicantia are most variable, both because the sample is smaller and because

they include some which are of very recent origin and are presumably still in the initial phase of very rapid regression. These probably account for the shoulder in the 'young' frequency curve at 4·75 cm.

The most striking of these frequency distributions is that for 'old' corpora albicantia, which is very symmetrical and suggests that no more than 30 out of 2339 corpora (1·3 %) have either been wrongly allotted to this group instead of to the 'medium' group, or have disappeared completely. This is the extent of the alteration required to make the curve quite symmetrical, and it may well be the result of chance. The fact that the curve for this group is symmetrical and non-skewed confirms that these corpora represent the final stage of regression in size and that very few are less than 1 cm. in diameter. If 'old' corpora continued to regress in size, but some of those under 1 cm. in diameter were being missed, then the frequency curve should be skewed, with a steeper slope where the lower sizes are
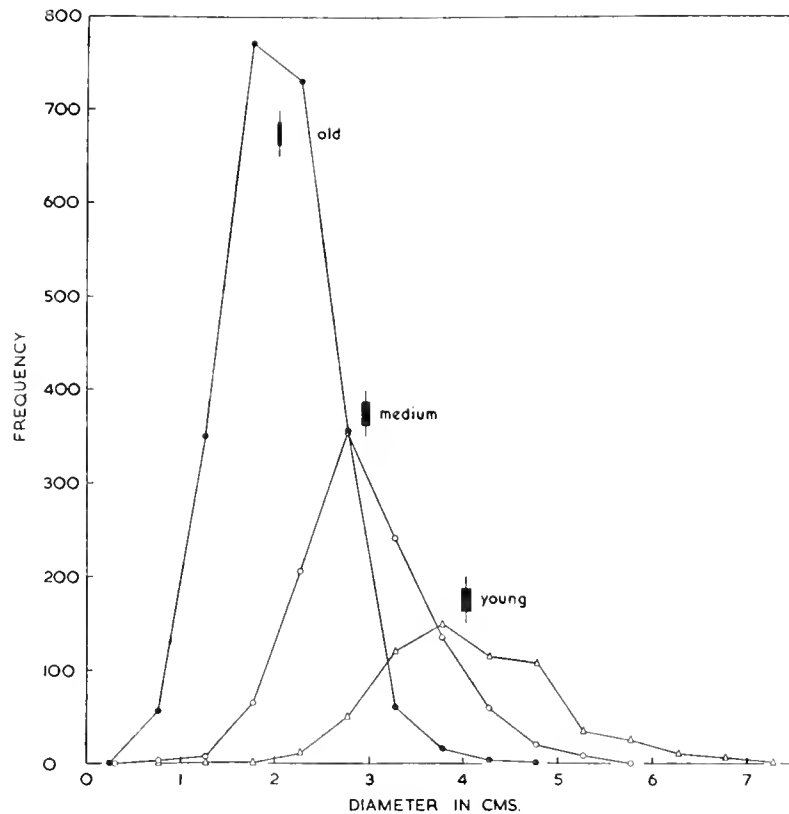
Text-fig. 16. Size frequency distribution of 'young', 'medium', and 'old' corpora albicantia. Means ± 2 s.e. are indicated.

cut off. In fact it is symmetrical, like the frequency curve of corpora lutea. This material is convincing direct evidence of the persistence of corpora albicantia throughout life in the female fin whale.

This conclusion can be checked by two methods which involve only the size of the corpora and not their morphological type. In the first method the size frequency distributions in whales with 1, 2, 3, ... to over 30 corpora albicantia have been plotted separately. The modal diameter decreases as the proportion of old corpora albicantia in the samples increases. In Text-fig. 17 the modal diameters have been plotted against the number of corpora albicantia for those groups in which the sample size was over 40. The modal diameter decreases in the first groups from about 4 cm. in the single corpus group to 2 cm. in the groups with over 11–12 corpora; the mode then remains more or less the same for the remainder of the groups. If corpora continued to regress in size until they finally disappeared then the modal size should continue to decline instead of stabilizing at 2 cm. This is both the mean and modal size of the 'old' group of corpora albicantia.

A second method is to take all the corpora albicantia up to 3 cm. in diameter, and to calculate the proportions in the size groups 0–1, 1–2 and 2–3 cm. for each of the groups of females with 1, 2, 3, …, to over 30 corpora albicantia. The percentage composition of the 0–3 cm. groups is plotted in this way in Text-fig. 18. If there is complete regression in size of the corpora albicantia one would expect, as more corpora accumulate, a progressive and continued increase in the percentage of corpora in the
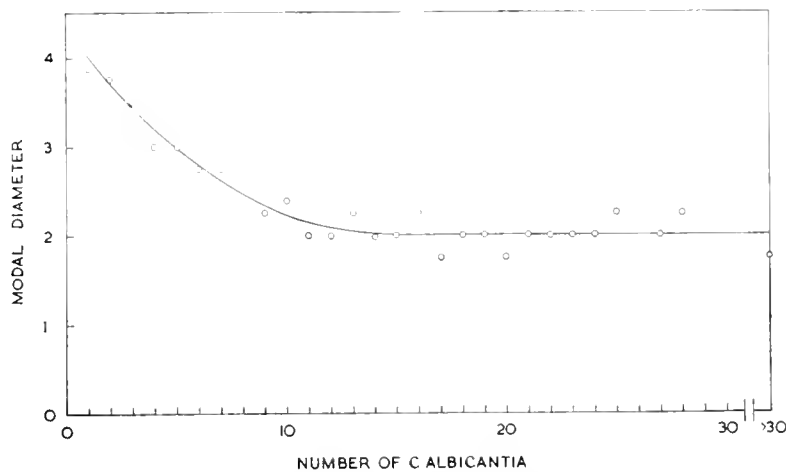
Text-fig. 17. Variation in modal diameter of corpora albicantia with increasing corpora numbers.
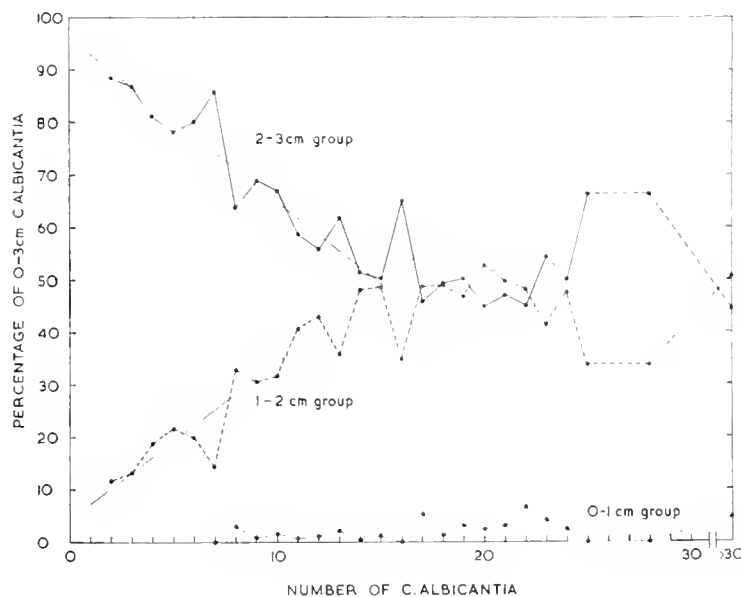
Text-fig. 18. Variations in percentages of corpora albicantia in different size groups, with increasing corpora numbers.

0–1 and 1–2 cm. groups, and a decrease in the proportion of 2–3 cm. corpora, until at the higher corpora numbers the great majority are in the 0–1 or 1–2 cm. group. Text-fig. 18 shows that there is initially a rapid decrease in the proportion of 2–3 cm. corpora and a complementary increase in the proportion of 0–2 cm. corpora, but when about fifteen corpora albicantia have accumulated this change in the proportions of corpora albicantia ceases, and the numbers of 0–2 and 2–3 cm. corpora are nearly equal. The numbers of 0–1 cm. corpora remain small and do not show any significant increase. This means, as before, that the corpora albicantia regress in size to a modal diameter of 2 cm. and then no

further. Those corpora included in the 'old' group are, therefore, assumed to be fully regressed corpora, at least as regards size.

Clearly there is in general no complete regression of corpora in respect of size. Nor is there any evidence that the corpora shrink to a mean diameter of 2 cm. and a weight of about 5 g. and then become indistinguishable from the ovarian stroma by further loss of pigment. Corpora albicantia of this size can easily be identified even if they appear to have lost all their pigmentation, because their white avascular connective tissue stands out against the darker colour of the ovarian cortex. Nor is there any histological evidence for eventual disintegration and resorption by phagocytes, because no intermediate conditions have been observed. A consideration of the rate of formation of 'old' corpora albicantia lends further support to this conclusion (Text-fig. 22). Once they begin to form the increase in their number is linear showing that they accumulate at a constant rate which shows no sign of decreasing, at least up to a total corpora number of 30 or 40. If their life-span was less than the period covered by the material then their numbers might be expected to approach or to reach an upper limit at which loss was balanced by replacement.

It has already been established that the mean diameter of the fin-whale corpus luteum of pregnancy is 11·44 cm. (p. 356), the mean diameter of the corpus luteum of ovulation is 8·28 cm. (p. 356) and the mean diameter of the accessory corpora lutea is 3·88 cm. (p. 361). The latter group comprise only 3·7% of all corpora lutea examined, and their effect on the ensuing discussion is negligible. The corpora albicantia, which represent former corpora lutea of all three types, have been shown to regress to a mean size of 2·01 cm.

Table 4. *Mean diameter of corpus luteum and mean or modal diameter of fully regressed corpus albicans for five species*

	Mean or modal size (cm.)		Percentage regression
Species	Corpus luteum	Corpus albicans	
B. physalus	11·44	2·0	82·6
B. musculus	13·75	2·4	82·6
M. novaeangliae	11·98	c. 1·9	84·1
P. catodon	7·25	1·25	82·8
G. melaena	c. 5·0	c. 0·85	83·0

The frequency distribution of the diameters of corpora lutea of pregnancy is a symmetrical curve with the mean approximating to the mode and it is likely that the curve for corpora lutea of ovulation would be similarly symmetrical if there were more records, although the size range is greater. Unfortunately, we have few records of corpora lutea of ovulation, because they persist for such a short period and are mostly produced during the months before the present antarctic whaling season begins (see p. 437). If the numbers of corpora lutea of pregnancy produced are equal to the numbers of corpora lutea of ovulation, then a size frequency curve for all corpora lutea would have a mean which would be the resultant of the mean diameters of the corpora lutea of ovulation and pregnancy, in this hypothetical case 9·86 cm., which means that corpora lutea as a whole regress to 2 cm., that is by 79·7% of their initial diameter. On the other hand, if on average only one out of three ovulations is followed by pregnancy the resultant mean size of all corpora lutea will be 9·33 cm. and the percentage regression will be 78·6% of the initial diameter. It should be noted that the difference between the amount of regression in these two cases is only 1% and even with a ratio of four unsuccessful ovulations to one pregnancy the variation is only increased to 1·7%. Conversely, if all ovulations were successful and followed by pregnancy the percentage regression would be 82·6%. The range, from a ratio of four unsuccessful ovulations to one pregnancy, to no unsuccessful ovulations, is only 4·6%.

There are reasons for believing that in the fin whale there are about two unsuccessful ovulations to one pregnancy (see pp. 459–63) and this appears also to be the case in *Globicephala melaena* (Fisheries Research Board of Canada. Annual Report, 1953).

This regression in diameter, in the second and most likely case, corresponds to a decrease in weight from 500 to 5 g. (from Text-fig. 8), that is a percentage decrease of 99%. Because the density does not change during regression this will equal the percentage decrease in volume.

Unfortunately we do not have material directly representative of the contribution of the corpora lutea of ovulation to the accumulating corpora albicantia, but as has been shown, the maximum variation from the true percentage regression is unlikely to be more than 4·6%. In order to compare material from different species we can only compare the size of the corpus luteum of pregnancy and the size of the fully regressed corpora albicantia, derived from both corpora lutea of pregnancy and corpora lutea of ovulation. The results might be expected to vary slightly according to the ratio of
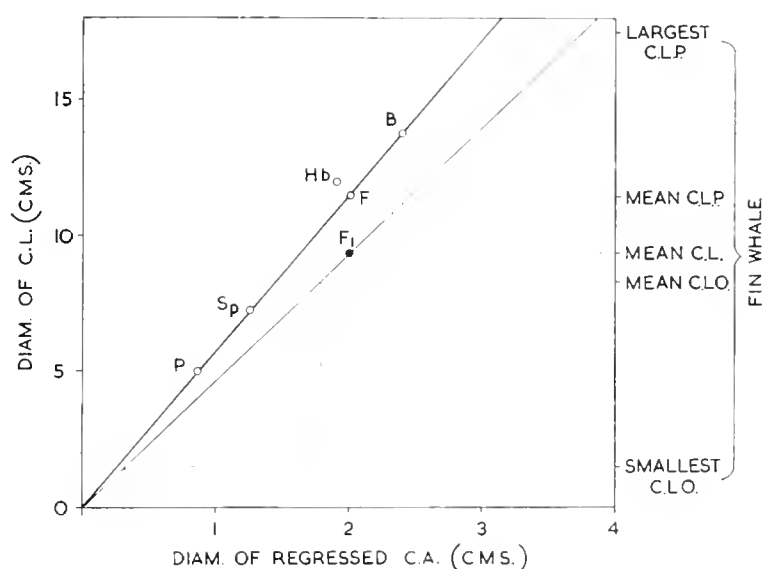
Text-fig. 19. Mean diameters of corpus luteum of pregnancy and mean or modal diameters of fully regressed corpus albicans (blue, fin, humpback, sperm and pilot whale). For the fin whale the estimated mean size of corpora lutea of pregnancy and ovulation is shown (F_1), and method of estimating regressed size from initial diameter is indicated by dotted lines.

ovulation and pregnancy corpora lutea although with small samples the experimental error will be greater than this variation. In Table 4 and Text-fig. 19 the mean sizes of the corpus luteum of pregnancy and the mean sizes of fully regressed corpora albicantia are given for five species of whales. The data for the blue whale, humpback whale and sperm whale were obtained in the same way as the fin whale data, though the material for the last two species is less abundant. The figures given for *Globicephala melaena* are very approximate and are derived from the very few measurements given by Harrison (1949). Nevertheless, the values for the percentage regression in diameter fall within the range 82·6–84·1%. Mansfield (1958) gives measurements of 30 corpora lutea (mean diameter 24·4 mm.) and 155 corpora albicantia (mode 6 mm.) of the Atlantic walrus, *Odobenus r. rosmarus*. These suggest that the walrus corpus luteum regresses by about 75·5% in diameter, but the method of measurement may be slightly different. For the two whale species for which the most observations are available the percentage regression is identical.

This table shows that on average corpora lutea from 5 to 13·75 cm. in average diameter, of very different cetacean species, regress by a similar amount to a final size which is proportional to the initial size. From this it follows that corpora lutea of varying sizes in a single species should regress

on average to a similar fixed percentage of their original size. Presumably this is determined by the initial size of the graafian follicle and the connective tissue framework, and it is conceivable that the corpora of ovulation might regress to a different percentage of the initial size, owing to a possible initial difference in the amount of connective tissue in the gland.

We have material which enables us to check this hypothesis. It has been shown that the 'old' corpora albicantia represent the final products of regression of corpora lutea both of ovulation and pregnancy, and we have records of the size frequency of 2339 'old' corpora albicantia which enables a very accurate frequency curve to be drawn. One assumption must be made—that corpora lutea of ovulation and pregnancy are formed in the approximate ratio 2:1, but we can also test the hypothesis using other ratios. There are good reasons, given later in this paper (see pp. 459–63), for believing that this assumed ratio is in fact correct. This means that the mean diameter of all corpora lutea will be 9·33 cm. and the upper regression line in Text-fig. 19 must be amended to the lower for the fin whale (F_1) at least.

In addition to the size frequency distribution of 'old' corpora albicantia there are records of the size frequency of 523 corpora lutea of pregnancy (Text-fig. 7). By using the graph (Text-fig. 19) these size frequencies have been converted into the corresponding size frequencies for the resulting corpora albicantia (Text-fig. 20, curve B). If both types of corpora regress to the same extent then the frequency curve for all 'old' corpora albicantia represents the sum of the frequency curves of 'old' corpora albicantia derived from corpora lutea both of ovulation and of pregnancy.

For direct comparison these frequencies are converted into percentages. The intervals for the calculated corpora albicantia of pregnancy are different from the intervals for total 'old' corpora albicantia because the peak value of this curve is almost exactly 2·5 cm. If it were drawn to the same intervals as the total 'old' corpora albicantia the result would be to convert a symmetrical curve to a skewed curve, so the points are displaced by 0·25 cm. with reference to the total 'old' corpora albicantia. The true frequency curve for corpora lutea of pregnancy (Text-fig. 7) has a shoulder at a size corresponding to the interval 2·0–2·5 cm. in corpora albicantia and this has been drawn in to make the curve more symmetrical (Text-fig. 20, curve B).

If the old corpora albicantia curve is the sum of fully regressed corpora lutea of ovulation and pregnancy in the ratio 2:1, it may be considered to be composed of three units, and the corpora albicantia of ovulation and pregnancy as two and one units respectively. In Text-fig. 20 the corpora albicantia of pregnancy (B) total 100% and total 'old' corpora albicantia (A) are converted to equal 300%. If our assumption is correct a symmetrical curve totalling 200% (C) should be obtained by subtracting the corpora albicantia of pregnancy frequencies (B) from the total 'old' corpora albicantia frequencies (A). This curve (C) should have a mean, mode and size range approximating to these values for the sample of corpora lutea of ovulation sizes converted to corpora albicantia of ovulation sizes. In Text-fig. 20 the size range, mean value and two standard errors (D) for the calculated corpora albicantia of ovulation are shown for comparison because the sample is too small to give a smooth curve. In fact, curve C is symmetrical, and its mean and mode approximate very closely to the mean corpus luteum of ovulation diameter converted to corpus albicans of ovulation size.

The hypothesis can be tested with other ratios of corpora lutea of ovulation and pregnancy, but none gives such a good fit. For instance, on the assumption that the numbers of corpora lutea of ovulation and corpora lutea of pregnancy are equal, curve A is drawn so as to total 200%, and curve B as 100%, so that curve C should equal 100%. Curve C is again symmetrical with a peak at 1·8 cm., but the size range is much less than expected (from D) and part of curve B falls outside curve A, which is improbable.

It is, therefore, probable that the 'old' corpora albicantia represent fully regressed corpora lutea of

which about two-thirds are contributed by corpora lutea of ovulation and one-third by corpora lutea of pregnancy. The regression is to a constant proportion of the former size, and corpora lutea of ovulation and pregnancy do not appear to differ in this respect. A negligible proportion are missed in the routine examination.

It has been stated that the smallest corpus albicans which is expected to be observed in the routine examination is about 7 mm. in diameter. Below this size it is probable that some will be missed because the thickness of the slices is 5 mm. On the basis of the regression factor established above a corpus albicans of 7 mm. corresponds to a corpus luteum of 3·2 cm. in diameter and it is therefore likely that the majority of, but not all, corpora albicantia representing former corpora lutea under 3 cm. in diameter, are missed in the routine examination.
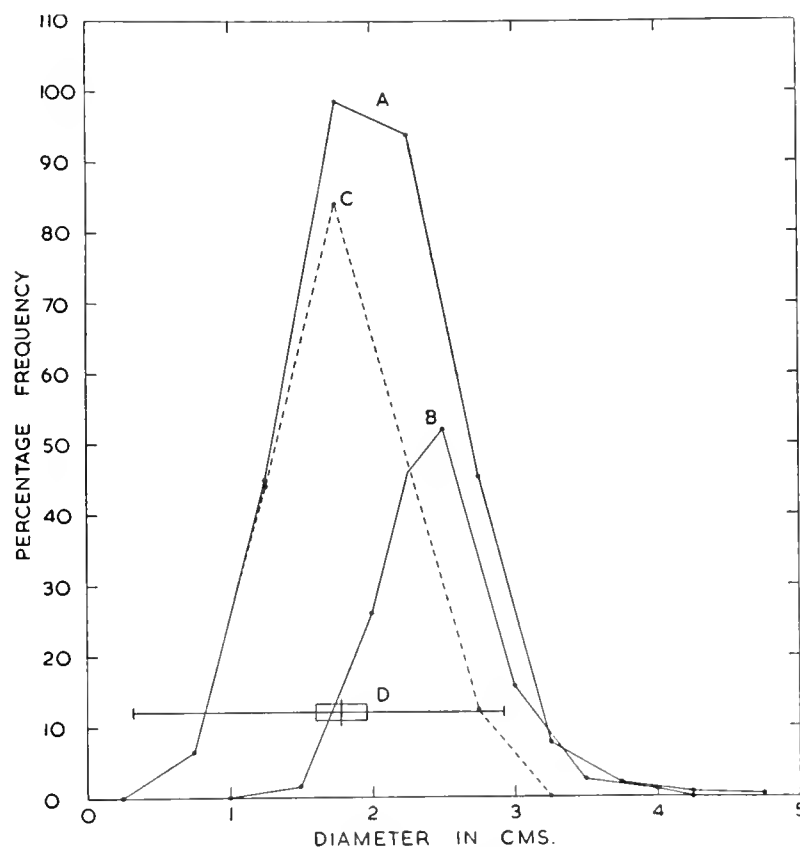
Text-fig. 20. A, size frequency distribution of all 'old' corpora albicantia; B, size frequency distribution of 'old' corpora albicantia of pregnancy (calculated from Text-fig. 19); C, resulting size frequency distribution of 'old' corpora albicantia of ovulation; D, calculated mean diameter ± 2 s.e., and size range of 'old' corpora albicantia of ovulation (see text for explanation).

There was no corpus luteum of pregnancy smaller than 3 cm., but four out of 59 corpora lutea of ovulation were under this size, that is, 6·8%. In terms of total 'old' corpora albicantia this will represent 4·5% (because there are about two corpora lutea of ovulation to one corpus luteum of pregnancy). The accessory corpora lutea, some of which do not represent ovulations, range from 0·5 to 8·5 cm. in diameter with a mean of 3·88 cm. so a larger proportion of them will be unrepresented by observable corpora albicantia. In fact 11 out of 26 were under 3 cm. in diameter, that is 42·3%, and since accessory corpora lutea comprise about 3·7% of all corpora lutea this amounts to about 1·6% of all 'old' corpora albicantia. The accessory corpora lutea which are expected to be observed when fully regressed, that is to say those which are initially 3 cm. in diameter or larger, amount to 2·1% of all corpora lutea.

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Thus, there is no permanent record in the form of fully regressed corpora, of 4·5% of corpora lutea of ovulation and pregnancy in the ovaries. On the other hand, 2·1% of the 'old' corpora albicantia are expected to represent accessory corpora lutea, so there is a net loss of 2·4%. So far we have been considering fully regressed corpora, but 42·5% of all corpora albicantia in this sample of 4065 were either 'young' (15·5%) or 'medium' (27·0%) and had not fully regressed. The corpus luteum which would eventually be represented by a fully regressed corpus albicans of 7 mm., can be shown in these two groups to have regressed to 1·4 or 1·0 cm. respectively, which means that the effective number of lost corpora albicantia considered as a percentage of all corpora albicantia ('young', 'medium' and 'old') is considerably less than 2% and probably nearer 1%.

This is such a small fraction of the total that it is probably within the observational error and it will be assumed for the purposes of applying the corpora counts to age-determination that all ovulations, whether successful or not, are recorded permanently in the ovaries by corpora albicantia.

Accumulation of corpora albicantia

It has now been established that corpora albicantia of the three groups, 'young', 'medium' and 'old' represent stages of regression. It might be possible to obtain an estimate of the absolute rate of regression by examining the proportions in which they occur and the relative rates at which they accumulate.

For 393 pairs of ovaries with three or more corpora albicantia collected in the season 1955/56 the mean numbers of 'young' corpora albicantia for pregnant and non-pregnant females are $1·522 \pm 0·125$ and $1·586 \pm 0·185$ respectively. There is no significant difference between these values and the combined mean value is $1·544 \pm 0·104$. Individual females had up to five 'young' corpora in the ovaries; only 15 out of 393 had more than three. Unfortunately, there are only nine records of lactating females, and they give a mean number of $1·778 \pm 0·688$ 'young' corpora albicantia. This is not significantly different from other samples, but the large standard error means that there could be a difference of up to one 'young' corpus albicans between lactating and non-lactating females.

At the time of writing the 1956/57 sample has not yet been fully examined, but for 251 pairs of ovaries which have been sliced (and have three or more corpora albicantia) the mean numbers of 'young' corpora albicantia for pregnant and non-pregnant females are $1·473 \pm 0·126$ and $1·545 \pm 0·318$ respectively. There is thus no significant difference between the mean numbers of 'young' corpora albicantia present in each of these two seasons.

Using the 1955/56 data it is also possible to compare the mean number of 'young' corpora albicantia of females in part of the former sanctuary (area I),[1] with the mean number of 'young' corpora in the older whaling areas (material mainly from area II). In area I the mean is $1·674 \pm 0·200$ and in the other areas it is $1·507 \pm 0·121$. Again the difference is not significant. The area I stock has been only slightly fished and the annual mortality rate appears to have been about 10% prior to 1956, whereas it has been found that in the older whaling areas the mortality rate is possibly over twice as high (International Commission on Whaling, Eighth Annual Report, p. 24).

It would appear then, that there is little change in the average number of 'young' corpora albicantia produced from year to year, and that even great changes in the condition of the stock have had no significant effect on the mean number of 'young' corpora in the ovaries. This is a point of considerable importance which will be referred to later (p. 384) in connexion with the constancy of the average annual increment of corpora albicantia.

Considering now those ovaries in the 1955/56 collection containing five or more corpora albicantia (sample size 323) we can determine the mean number of 'medium' corpora present. This is $3·220 \pm$

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[1] There are six antarctic whaling 'areas'. Area I is in the South-east Pacific Ocean (60–120° W.).

0·206, and the ratio between the mean numbers of 'young' and 'medium' corpora albicantia is therefore 1:2·085. We will assume that it is 1:2.

'Young', 'medium' and 'old' corpora albicantia represent consecutive stages of regression and, if the sampling is representative, the average duration of these stages should be proportional to the frequency of each group, since they do not disappear. The 'medium' corpora albicantia are twice as common in the samples as the 'young' corpora.

The antarctic pelagic whaling season for fin whales lasted 58 days or 0·16 years in 1956, and 69 days or 0·19 years in 1957, 1958 and 1959. It is, therefore, reasonable to suppose, for present purposes, that sampling is instantaneous and at yearly intervals. The majority of corpora albicantia are formed several months before the sampling period and *very few* actually during the sampling period (see below, pp. 450–53). If the average duration of the 'young' stage extends over x sampling periods, then the 'medium' stage, because it is twice as frequent, persists over $2x$ sampling periods. If sampling were not restricted to a short annual period then the actual ratio of 'young' to 'medium' corpora in the samples might be very different from 1:2, and the actual duration of 'young' corpora (in terms of months, rather than sampling intervals) may be much less than half the duration of the 'medium' stage.

An example will make this point clearer. Suppose the average month of formation of corpora albicantia is August. Then the average sampling date (in February) is some 6 months later and for 'young' corpora albicantia to be fully represented in the samples they must, on average, persist in this stage for over 6 months. In the simplest case, in order to fit the data a corpus albicans formed in August must be present as a 'young' corpus albicans only in the first sampling period, and as a 'medium' corpus albicans in the two succeeding annual sampling periods. Whereas, on average, the 'young' stage need last at a minimum for just over 6 months (less than 18 months at a maximum) in order to be represented in only one sampling period, 'medium' corpora can last as long as 35 months (but not less than just over 12 months) in order to be represented in two sampling periods.

It is, however, known that 'young' corpora albicantia do not disappear during pregnancy and because ovulations do not occur during pregnancy the average duration of this stage of regression must be at least 10 or 11 months, though the rate of regression may be more rapid during lactation (see p. 434).

In estimating the average annual increment of corpora it is not, therefore, the absolute duration of each stage, but the relative duration in terms of the number of sampling periods that occur during each stage which is important.

Because the relation between the average numbers of 'young' and 'medium' corpora approximates to a simple ratio, in the equation below t must approximate to a whole number.

Let n = observed average number of 'young' corpora albicantia;

t = duration of this regression stage in sampling intervals;

a = annual increment (to be ascertained).

Then $a = n/t$, and the shorter the duration the larger must be the annual increment (or vice versa) to provide the observed value of n.

The parameter n is known; t must be sought by trial and testing with other evidence but is assumed to be a whole number (not a fractional value), for the reasons given above.

If $t = 1$ then $a = 1·544 \pm 0·104$;

$t = 2$ then $a = 0·772 \pm 0·052$;

$t = 3$ then $a = 0·515 \pm 0·035$;

$t = 4$ then $a = 0·386 \pm 0·026$.

Values of t higher than 2 are excluded by virtue of the sexual cycle of the mature female and the

7·2

high percentage of these females which are found to be pregnant (p. 455); this requires appreciably more than one ovulation in 2 years.

The second case ($t = 2$) is a possibility, but for a 2-year breeding cycle it gives a ratio of ovulation corpora to pregnancy corpora of approximately 1:2. This does not fit the conclusions about the percentage regression factor and the data on the size frequency of fully regressed corpora albicantia (p. 374) which indicate a ratio of 2:1; nor is it in agreement with the evidence from the sexual cycle (p. 460).

The first and simplest case ($t = 1$) appears much the most probable. For a 2-year breeding cycle it gives a ratio of ovulations to pregnancies of approximately 2:1, which is in agreement with the conclusions drawn from the size frequency of fully regressed corpora (p. 374). It is also in agreement with estimates of the average annual rate of ovulation obtained by other quite independent methods (p. 460) It also means that on average the regression to 'old' corpora albicantia takes about 3 years, which was the opinion of Van Lennep (1950, p. 596), based on histological grounds. This evidence strongly suggests that the average annual increment of corpora is about 1·5, although on the present evidence a possible increment of 0·75 cannot be completely excluded. Further support for $t = 1$, comes from the growth estimates (on pp. 413–415, and Text-figs. 38 and 39).

In Text-figs. 21 and 22 the mean numbers of 'old' and recent (that is 'young' and 'medium') corpora albicantia for different total corpora numbers have been plotted and curves fitted to them. It is then apparent that the average number of recent corpora continues to increase with age. One possible explanation of this is that the average annual production of corpora albicantia increases with age and as this has a very important bearing on the question of age-determination it must now be dealt with.

Other considerations being equal the formation of 'old' corpora albicantia should lag about 3 years (strictly three sampling periods) behind the production of 'young' corpora, but should take place at the same rate. The regression line describing the rate of accumulation of 'old' corpora should therefore have a slope of 1·0. In fact the regression line (calculated by the method of least squares and ignoring the first six points) is described by $y = -3\cdot433 + 0\cdot885x$, when y is the number of 'old' corpora albicantia, and x is the total number of corpora albicantia. This gives an intercept on the x-axis at 3·88, suggesting that if 'young' corpora take three sampling periods to regress to 'old', then the annual increment in the first 3 years after puberty averages about 1·3. We know that there are in the material 88 females in their first pregnancy, and these had a mean number of $1\cdot420 \pm 0\cdot146$ corpora, which is in close agreement. The intersection of the two curves in Text-fig. 21 is at 8·9 corpora, when 4·45 recent corpora and 4·45 'old' corpora have formed. This implies that during the time it takes for 4·45 'old' corpora to accumulate a further 4·45 'young' and 'medium' corpora are formed and that 'old' corpora are being added at about the same rate as 'young' corpora are formed. This suggests that 'young' corpora form at the rate of about 1·48 per year.

The average number of recent corpora then increases from 4·45 at this intersection to 5·8 when a total of 20 corpora have accumulated and to 7 when a total of 30 corpora have accumulated, and so on. This apparently corresponds to increases in the annual rate of production of corpora from 1·3 just after puberty to approximately 1·5, 1·9 and 2·3 at later ages. In terms of the number of ovulations per 2-year cycle it implies a 50% increase over this age range from about 3 to over 4·5, that is more than one extra ovulation per cycle.

There is some evidence that the frequency of dizygotic twinning increases with age as a result of multiple ovulations (Kimura, 1957), but only by a few per cent. Accessory corpora lutea amount to only about 4% of all corpora lutea and multiple ovulations increase only slightly with age (see p. 454). Nor is there any evidence for any other kind of increase in the ovulation rate. The percentage of mature females with corpora lutea in the ovaries remains remarkably constant with increasing age (Text-fig. 52).
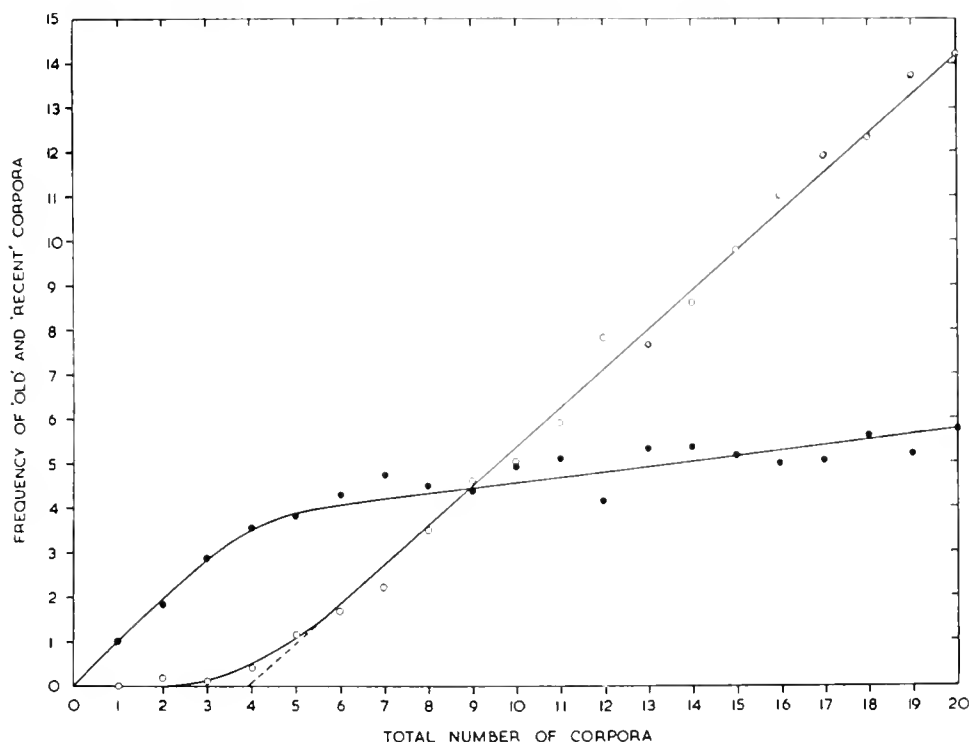
Text-fig. 21. Changes in the mean number of 'old' (white circles) and recent ('young' and 'medium')
corpora albicantia (black circles), with increasing corpora numbers.
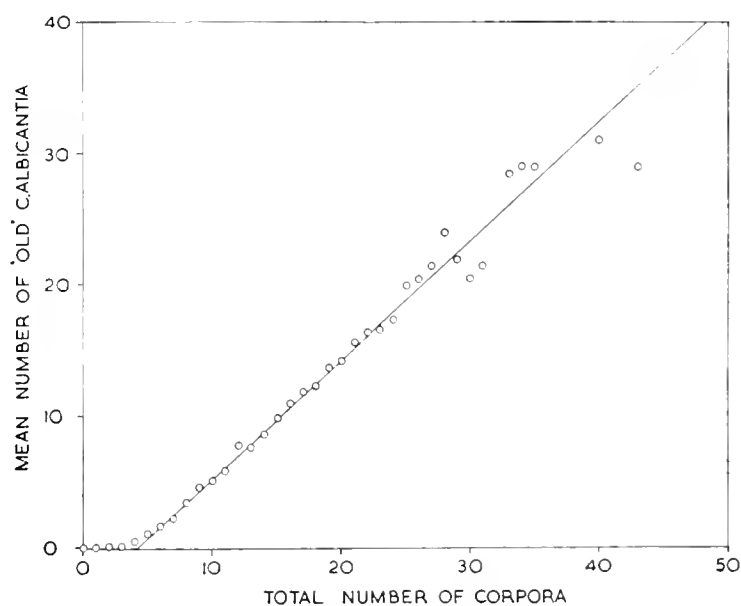
Text-fig. 22. Changes in the mean number of 'old' corpora albicantia with increasing corpora numbers.

Two possible explanations of this rise in the number of recent corpora albicantia associated with increasing age could be advanced. One is that there is a progressive human error in the counts, a tendency to overestimate the number of recent corpora as the total number of corpora increases. This can be checked and does not account for this large increase.

Another explanation is that the rate of regression becomes progressively slower with age, the duration of the 'young' and 'medium' stages being longer and the number of corpora in these stages increasing. It is possible to apply a test to this hypothesis, because if the rate of regression is slower then the

size of corpora albicantia of similar ages should be greater in older whales. Dr Mackintosh has shown me some unpublished figures he worked out for the average sizes of corpora albicantia, based on a large number of measurements. He was able to show that the average size of the nth largest corpus albicans does in fact increase with age, that is, with increasing corpora number. For example, when there are 10 corpora albicantia the tenth largest is smaller than the tenth largest when there are 20 corpora albicantia. This finding has been inexplicable up to now, because the most obvious interpretation, that the size of the corpus luteum and therefore of its products increases with age, is known to be inapplicable (see p. 357). I am indebted to Dr Mackintosh for enabling me to refer to this work.

It appears then that this apparent increase in the rate of ovulation is due to the lengthening of the period occupied by the regression of the corpus albicans in older whales. A correction has, therefore, been made, by assuming that 'old' corpora albicantia accumulate at the same rate as 'young' corpora albicantia form. This assumption is valid if the duration of the regression period is constant and there is no human error in the counts of recent corpora, and no increase in the rate of ovulation. The last qualification is not quite correct, but may be ignored for the moment.

A corrected regression line of slope 1·0 was, therefore, drawn through the intersection point of the two curves shown in Text-fig. 21, giving an intersect on the x-axis of 4·45, and an estimate for the average annual increment of corpora of 1·48. This figure is likely to be a little high because it does not allow for any increase in the regression period while the first nine corpora are accumulating; nor are we justified in assuming that there is no increase in the ovulation rate with age. There is in fact a slight rise in the incidence of multiple ovulations. Taking into account all the evidence the best estimate of the average annual rate of accumulation is between 1·4 and 1·5.

Taking the duration of the 'young' and 'medium' stages in the regression of corpora to be about 1 and 2 years respectively, the mean sizes of the corpus luteum, 'young', 'medium' and 'old' corpora albicantia, may be plotted on semi-logarithmic paper. For both diameter and weight the initial regression is very rapid, corresponding to the change from glandular tissue to collagen, and is succeeded by slower regression which is apparently exponential (that is to say, the points fall on a straight line) until the fully regressed stage is reached.

CORPORA ABERRANTIA

In addition to the types of normal corpora albicantia and corpora lutea, which have been described and shown to represent stages in the regression of ovulation and pregnancy corpora lutea, a very small number of other corpora are present in fin-whale ovaries.

During the examination of the 1953/54 ovaries four unusual types of pigmented bodies were identified. One very distinct type, small and bright orange-yellow in colour, is more properly a corpus atreticum and is not considered to represent a former corpus luteum. The other three main types have yellow or buff pigmentation. They were termed corpora aberrantia and distinguished by the adjectives 'yellow', 'buff-cellular' and 'yellow and white'. In the routine examinations of part of the 1955/56 collection further observations were made on the incidence of these types. Out of a total of 2655 corpora albicantia and corpora aberrantia (corpora atretica excluded) only 37 (or 1·4%) were corpora aberrantia. The 'yellow' type comprises 0·7%, 'buff-cellular' 0·6% and 'yellow and white' 0·1%. They were present in 34 out of 273 pairs of ovaries (12·5%).

All appear to have developed from ruptured follicles (Text-fig. 23b and c), but it is difficult to establish the cause of their formation and their fate is uncertain.

'Yellow' corpora aberrantia

The size range of 17 corpora of this type is from 1·3 to 3·3 cm. in mean diameter, average 2·12 cm. They range in colour from a uniform bright lemon-yellow to primrose-yellow in both fresh and fixed material. In shape they are usually irregular or amoeboid, suggesting a collapsed follicle which has re-expanded only slightly, and often have a conspicuous stigma (Text-fig. 23 a).

In histological preparations of formalin- or Bouin-fixed material, paraffin embedded, they are seen to consist of a homogeneous collagenous matrix (staining blue in Mallory, green in Masson's trichrome, and pink in Haematoxylin and Eosin) with uniformly scattered vacuoles representing dissolved lipoids. In material which has been fixed in Zenker-formol (Helly) and post-osmicated (Pl. VII, fig. 3), darkly stained lipoid material is seen to be distributed in discrete globules throughout the matrix, but there are concentrations of lipoid material at the periphery. In contrast to the normal corpus albicans the outline is very definite and there is no penetration by blood vessels into the lobes of the corpus.
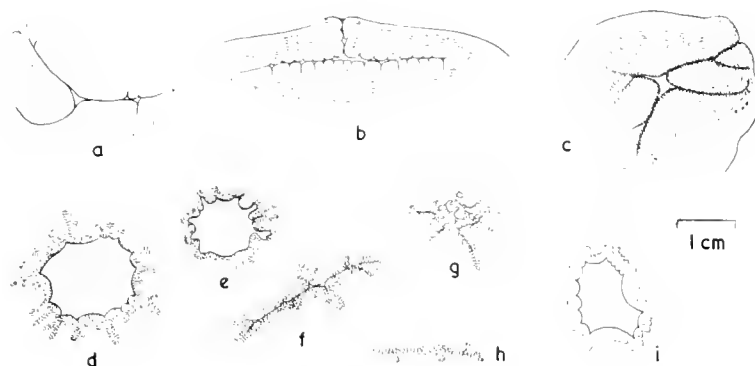
Text-fig. 23. Morphology of corpora aberrantia (a–c) and corpora atretica (d–i).

'Buff-cellular' corpora aberrantia

The mean size of fifteen corpora of this type is 2·14 cm., ranging from 1·3 to 3·2 cm. in diameter. Macroscopically the colour is a pale buff with a slightly darker layer next to the trabeculae marking the folding of the original follicle and dividing the corpus into narrow compartments or cells (Text-fig. 23 b). These corpora are very similar to the 'yellow' corpora aberrantia in histological structure, but differ in their more regular outline and in the distribution of the pigment. They are thrown into many small, meandrine folds reminiscent of a miniature corpus luteum and like the corpus luteum give the impression of a re-expansion to occupy a roughly spheroidal or ovoidal shape. As in the other corpora aberrantia there is very little vascularization and the blood vessels are confined to the narrow trabeculae. In histological preparations the pigmentation is heavier in a layer adjacent to the trabeculae.

'Yellow and white' corpora aberrantia

The size range of three corpora of this type is 2·2–2·5 cm., with a mean diameter of 2·3 cm. The colour is white, with a deep orange-yellow pigment outlining the folds of the original follicle wall (Text-fig. 23 c). The pigment zone may be more extensive in parts, which then resemble the 'yellow' corpus aberrans. The outline in the three specimens available is more regular than that of the 'yellow' corpus aberrans but less regular than the 'buff-cellular' type. Histologically they are seen to be similar to the other two aberrant types, but have a much narrower and more densely pigmented zone near the trabeculae (Pl. VII, figs. 4, 6). As in these others the few blood vessels present are confined to the trabeculae.

One must conclude that these three types of aberrant corpora are very similar in size and structure and, therefore, in their origin and fate. In fact they may represent stages in the regression of one type. It is noticeable that all are more or less avascular bodies and appear to have undergone a type of lipid hyaline degeneration which is probably a direct result of the deficient vascularization.

It is not possible to say with certainty whether they persist as well-pigmented bodies for a long or short period. Nor is it known at which part of the breeding cycle they are formed, but they do not represent corpora lutea of pregnancy. All three types are found in females at puberty in addition to the more usual corpora albicantia. It seems likely that in fully mature females they form during or prior to the resting period and possibly again as accessory corpora lutea at the start of pregnancy. These bodies are present in $38 \cdot 4 \pm 19 \cdot 0 \%$ of resting females and $13 \cdot 2 \pm 7 \cdot 4 \%$ of pregnant females, but this difference is not quite significant at the 95% level. In the first half of pregnancy (foetus 0–1 m. long) $45 \pm 30 \%$ had one or two such bodies in the ovaries, and in the second half of pregnancy (foetus larger than 1 m.) only $7 \cdot 1 \pm 5 \cdot 8 \%$ had corpora aberrantia in the ovaries. Of those females with foetuses longer than 2 m. only $1 \cdot 7 \pm 3 \cdot 7 \%$ had such corpora. Of eleven lactating females none had such corpora aberrantia; some lactating females have anomalous corpora which are like corpora albicantia in their gross morphology but resemble corpora aberrantia in their histology. These observations suggest that their longevity as corpora aberrantia is probably little more than a year, and if some are formed at the same time as the corpus luteum of pregnancy then their life is only about 6 months. Their scarcity in terms of total corpora ($1 \cdot 4 \%$) and their relative abundance in terms of the proportion of ovaries showing them ($12 \cdot 5 \%$) supports this contention. In view of the fact that $38 \cdot 4 \pm 19 \cdot 0 \%$ of resting females had corpora aberrantia in the ovaries, but no lactating females had them, it would seem likely that these resting females had ovulated recently.

Corpora aberrantia are unlike corpora albicantia in their morphology, but the appearance of the collagen is similar to the pigmented collagen of corpora albicantia, except that it is much more heavily laden with lipids and pigment and the distribution of lipoid material is different. In view of their collagenous nature they cannot be regarded as functional, but are regressing bodies.

Corner, Bartelmetz and Hartman (1936) concluded that the corpora aberrantia, which they described in the rhesus monkey, were probably formed at the same time as corpora lutea of the cycle or of pregnancy. The whale corpora aberrantia now described are different from those described by Corner, Bartelmetz and Hartman which retain recognizable granulosa lutein cells and have a very noticeable network of capillaries. The latter are also much larger relative to the true corpora lutea than are the whale corpora aberrantia. These authors' type 3 corpora aberrantia appear to be very similar to the whale corpora atretica to be described below.

In most respects but size, the whale corpora aberrantia appear to agree with the description by Dubreuil and Rivière (1947, p. 83 and fig. 27, 1) of the 'mode de dégénérescence lipoide' in the human ovary.

CORPORA ATRETICA

In addition to the corpora lutea, corpora albicantia and corpora aberrantia, there are in fin-whale ovaries a number of small, bright orange-pigmented bodies. Laurie (1937, p. 244) described occasional yellow bodies in blue-whale ovaries. These were small ($1 \cdot 0 \times 0 \cdot 3$ cm.) and located deep in the ovary as compared with the other types of corpora which are most superficial. They were described as corpora atretica, the relics of atretic follicles. In the sample of fin-whale ovaries with altogether 2655 corpora lutea, albicantia and aberrantia there were a further 5% of corpora atretica. The greatest numbers were found in resting females (maximum 4) and in pregnant females with a foetus 1–3 m. long (maximum 8). In contrast to the corpora aberrantia no significant differences were found in the percentage occurrence of corpora atretica at different stages of the sexual cycle.

The mean diameter of those measured was 1·27±0·14 cm., but the modal diameter is 0·75 cm. and the true mean diameter is probably less than 1 cm.

All stages in the formation of these bodies have been observed, from a relatively large follicle (maximum 3·5 cm.) with slightly folded walls and a bright orange lining, through similar follicle stages, becoming more and more collapsed, and finally to small (4 mm.) stellate bodies or thin compressed orange streaks (Text-fig. 23 *d–h*). These undoubted chronological stages confirm that these bodies are corpora atretica. They have, therefore, been ignored in making the routine counts of corpora for purposes of age-determination (p. 466). There are also collagenous unpigmented corpora atretica in which the original follicle wall can be identified (Text-fig. 23 *i*).

The histology of one such pigmented body is illustrated in Pl. VII, figs. 5, 7. This shows it to be composed of tissue heavily laden with lipoid globules, but with very little collagenous material. It also shows the folding of the original follicle wall. These corpora atretica appear to be homologous with the 'corps lipoides' or 'formations spongiocytaires' of the human ovary described by Dubreuil and Rivière (1947, p. 83 and fig. 26 I). The third kind of atypical corpus of the rhesus monkey described by Corner, Bartelmetz and Hartman (1936) also appears to be in this category. It is largely composed of clear lipid-filled cells believed to be derived from the theca interna, but there is also a distinct zone of darker cells which appear to be granulosa cells. Brambell (1956, p. 501) described the corpora lutea atretica found in various mammals and states that, according to the majority of authors, these corpora originate by hypertrophy and hyperplasia of the cells of the theca interna after degeneration of the membrana granulosa. Owing to the small amount of whale material which has been examined histologically, it is not possible to say definitely whether whale corpora atretica are composed mainly of transformed theca interna cells or are developed from the granulosa layer.

CONCLUSIONS

Old, non-functional corpora lutea are termed corpora albicantia although the majority are still pigmented. There is no significant difference in the mean size of corpora albicantia of pregnant, non-pregnant and lactating females, which have a mean diameter of 2·5 cm. and a mean weight of about 10 g. The relation between weight and diameter for corpora albicantia is the same as that for corpora lutea and there is no significant alteration in density as a result of the changes in composition, appearance, and histology.

The morphological types of corpora albicantia correspond to the types of corpora lutea and in particular the incidence of vesicular or radiate corpora albicantia is not significantly different from the proportion of vesicular corpora lutea. This confirms that the incidence of vesicular corpora lutea of ovulation is not appreciably different from the incidence of vesicular corpora lutea of pregnancy.

Three age-groups of corpora albicantia have been identified on the basis of anatomical and histological changes. 'Young' corpora albicantia have a mean diameter of 4·01 cm. and a weight of 41 g.; the values for 'medium' corpora albicantia are 2·94 cm. and 15 g.; and for 'old' corpora 2·01 cm. and 5 g. The latter group has been shown to represent the final stage of regression when the corpus largely consists of unpigmented collagen.

Evidence which is considered to be conclusive has been presented showing that the corpora persist throughout the life of the individual. It appears that corpora lutea regress by a constant proportion of their initial size to a final size which is directly related to the initial size. Only the remnants of those corpora lutea originally under 3 cm. in diameter are likely to be missed in the routine examination of 5-mm. slices. This means that no more than 1% of ovulations are unrepresented by corpora albicantia large enough to be recorded in the conditions of the routine examination, and for practical purposes of employing corpora counts for age-determinations this may be regarded as negligible.

Some evidence bearing on the rate of accumulation of corpora albicantia is provided by examination of the absolute and relative numbers of these three types of corpora albicantia. There are no significant differences between the mean numbers of 'young' corpora albicantia in pregnant and non-pregnant females, nor between samples taken in consecutive years, the mean value being 1·54. Large variations in the mortality rates of populations of fin whales apparently have no significant effect on the rate of formation of corpora albicantia. It follows that if there are differences in the rate of accumulation they must be slight. The mean number of 'medium' corpora albicantia is 3·22, giving a ratio of 'young' to 'medium' corpora of 1:2. The average duration of the 'medium' stage is probably about twice as long as that of the 'young' stage and it is concluded that the 'young' corpora probably represent one year's increment, and on average take about 3 years to regress to 'old' corpora, which after the first few years accumulate at the same rate as the 'young' corpora. The mean number of 'young' and 'medium' corpora apparently increases with increasing total corpora number. Evidence is presented which strongly suggests that this is the result of a progressive retardation in the regression of corpora with increasing age of the female. Taking this into account the corrected estimate of the mean annual increment of corpora albicantia is between 1·4 and 1·5 although the possibility that this is in error by a factor of 2 cannot be excluded.

The possibility of gross morphological differences between corpora albicantia derived from corpora lutea of pregnancy and ovulation respectively, as suggested by Robins (1954) and Van Lennep (1950) has been examined and rejected. Peters (1939) claimed to have found such a macroscopically recognizable difference, based on differences in the colour and texture of the gland, in the arrangement of the connective tissue and the trabeculae. Although he examined 27 pairs of blue-whale ovaries and 57 pairs of fin-whale ovaries, with altogether 500 corpora, his counts establishing the proportions of the two groups of corpora are based on only 4 pairs of blue-whale ovaries (with 75 corpora in all) and 7 pairs of fin-whale ovaries (with altogether 97 corpora). He states that the darker group represent corpora of pregnancy and the lighter-coloured are corpora of the cycle. Since every corpus of pregnancy corresponds to a breeding period, and, therefore, on average to 2 years of life, the average number of ovulations per cycle can be obtained from the ratio of pregnancy corpora to ovulation corpora. For instance, if this ratio is 1:1 then there will be two ovulations per cycle. Peters's actual values for blue and fin whales are respectively 1·9 and 1·8 ovulations in 2 years.

Unfortunately Peters did not give precise details of these differences in his paper, but promised that they would be given in a later paper which was not completed before his death. No macroscopic difference attributable to different origin has been observed in the present material although several thousand corpora have been examined in detail. The only clear distinction which has emerged is that which is the result of age changes in the corpora. The differences between recent ('young' and 'medium') and 'old' corpora are similar to those indicated by Peters as distinguishing corpora of pregnancy and ovulation respectively.

It is instructive to assume that recent and 'old' corpora are derived from corpora lutea of pregnancy and ovulation respectively and see what figure is obtained for the rate of ovulation. The mean number of corpora albicantia per female in the 1953/54 and 1955/56 samples is 9·7. From Text-fig. 21 the mean numbers of recent and 'old' corpora albicantia at this corpora number are 4·6 and 5·1 respectively, giving a ratio of 1:1·1 and, according to Peters's hypothesis, an assumed 2·1 ovulations per 2-year cycle. The agreement with Peters's estimate of 1·8 is rather close when it is recalled that Peters's sample only contained seven whales and would have a correspondingly large variance. It is the author's opinion that this is probably the basis of Peters's estimate and this assumption, that recent and 'old' corpora are of different origin, is known to be incorrect.

It may be possible to identify corpora albicantia derived from corpora lutea of ovulation and pregnancy by quantitative histological examination. The rate of regression of corpora albicantia

appears to be related to changes in the thickness of the walls of the blood vessels. The relative thickness of the vessel walls may be a better quantitative index of the age of a corpus than is its diameter. Since the initial diameter of the corpus luteum of ovulation is only about two-thirds that of the corpus luteum of pregnancy, it is likely that for a given vessel-wall thickness the ratio of the percentage thickness of the vessel wall to the diameter of the corpus will be higher for those corpora albicantia derived from corpora lutea of pregnancy than for corpora lutea of ovulation and could perhaps be used to differentiate them. This is the only distinctive character which appears likely.

There are two other types of corpora which are found in fin-whale ovaries. These are the corpora aberrantia and corpora atretica. The former comprise 1·4% of all corpora albicantia and aberrantia and appear to develop invariably from ruptured follicles. They are more heavily pigmented than corpora albicantia and are also characterized by the absence of blood vessels from the lobes of 'luteal' tissue. Their frequency in different phases of the 2-year breeding cycle suggests that there is an ovulatory period at the end of lactation or the beginning of the 'resting' period when they are formed. These corpora are included in the routine counts of corpora albicantia for purposes of age-determination. The corpora atretica are formed from unruptured atretic follicles and are easily distinguished from true corpora lutea, albicantia or aberrantia. They are not included in the routine counts of corpora.

We have now dealt with the ovaries and the formation and subsequent history of the corpus luteum. It has been established that the corpora albicantia persist throughout the life of the female and from the numbers at the different stages of regression it appears that they accumulate at the rate of approximately 1·4–1·5 per year although the possibility of 0·7–0·75 per year cannot be excluded.

In the next part of this paper the accumulation of corpora albicantia up to the attainment of physical maturity will be discussed. Then the annual cycle and life-history of the fin whale will be described and the probable time and rate of ovulation will be discussed with a view to obtaining a second independent estimate of the annual increment of corpora and also of the range of variation.

ACCUMULATION OF CORPORA UP TO THE ATTAINMENT OF PHYSICAL MATURITY

The evidence presented in the preceding section suggests that the average rate of ovulation in a stock of whales does not vary appreciably from year to year or in different areas, but little has been said about the amount of variation shown by individual females. An examination of the accumulation of corpora up to a fixed point in the life-cycle, the attainment of physical maturity, is of relevance to this problem and gives us some additional evidence.

THE FREQUENCY OF CORPORA IN EARLY BALEEN GROUPS

It is shown below (p. 411) that, on average, females ovulate 1·42 times before becoming pregnant for the first time. In studying the amount of individual variation in the rate of accumulation of corpora, up to what is presumably a fairly regular age, the initial variation in the number of corpora in early age-groups, caused by the spread of ages at puberty, must be taken into account.

In the fin whale the evidence suggests that the majority of females ovulate for the first time at ages ranging from 3 to 8 years (see below, p. 407). Thus an 8-year-old female may be primiparous with one corpus luteum in the ovaries or have been mature for several years, with a correspondingly greater number of corpora in the ovaries. In any one age-group there can, therefore, be quite a wide range of corpora frequencies depending on the individual ages at puberty.

Hylen *et al.* (1955) give the frequencies of numbers of corpora in the ovaries of sexually mature female fin whales in baleen age-groups II–V. A description of this method of ageing may be seen in papers by Ruud (1940, 1945) and Ruud and Jonsgård (1950).

Sexual maturity in female fin whales is attained on average between baleen groups III and IV, with small numbers maturing in groups II and V. Consequently, the frequency distribution of corpora numbers in group V may be slightly truncated in the lower numbers, but will represent fairly accurately the frequency distribution of corpora numbers within early age-groups (Text-fig. 27) and can be compared with the frequency distribution of corpora at the attainment of physical maturity. Hylen *et al.* (1955) point out that baleen group V probably includes animals from more than one year class because it includes females with rather high corpora numbers. They suggest that 5–7·5% of individuals placed in group V are certainly older than 5 years of age, although the participation of older year classes may be greater than this. The mean number of corpora in baleen group V is 5·607 and, on the assumption that the average increment of corpora is 1·4–1·5 per year, the average age of group V would seem to be some 4 years later than puberty, suggesting, if puberty usually occurs in groups III and IV, that it includes several year classes.

A similar conclusion is reached on comparing ear-plug ages with baleen groups (see Text-fig. 55, p. 467).

THE NUMBER OF CORPORA AT THE ATTAINMENT OF PHYSICAL MATURITY

Growth in body length is accomplished in mammals by intercalary growth of the vertebrae, which occurs, as in other bones, at the zones of cartilage joining the epiphyses to the diaphyses. A whale is said to have attained physical maturity when the epiphyses are fused to the centra along the entire length of the vertebral column. When this happens linear growth of the vertebral column ceases, although growth in other dimensions may continue and the skull may continue to grow slightly. It has been shown that fusion of the epiphyses begins at both ends of the vertebral column and proceeds inwards. This process is more rapid from the tail end than from the head end so that fusion is usually completed in the anterior thoracic region, generally at the level of the fourth and fifth thoracic vertebrae.

Wheeler (1930, p. 411) showed that in female fin whales physical maturity is reached when about 15 corpora lutea and albicantia have accumulated in the ovaries. Peters (1939) came to a similar conclusion, but Brinkmann (1948) and Nishiwaki (1950*a*, 1952) concluded that the threshold of physical maturity was correlated with the accumulation of respectively 13 and 11·5 corpora. These discrepancies are probably the result of the application of different criteria of physical maturity, which will be discussed presently. Chittleborough (1955*b*, p. 321) suggested that physical maturity in the humpback whale coincides with the accumulation of some 30 corpora in the ovaries, but his criteria (Chittleborough, 1955*a*) differ from those of other workers and his relative growth curve (1955*b*, fig. 3) suggests that linear growth ceases when about 15–20 corpora have accumulated. The material of Symons and Weston (1958), although very sparse, suggests that physical maturity in the humpback whale is attained when between 8 and 20 corpora have accumulated and the criteria of maturity which they adopted are those used by the 'Discovery' Committee and the National Institute of Oceanography. Laurie (1937, p. 236) found a similar correlation in blue whales, physical maturity being attained at about 11–12 corpora.

'This accumulation of such a regular number of corpora lutea at such a landmark as physical maturity seems to leave no doubt not only that the corpora lutea persist up to and well beyond the age at which physical maturity is reached but also that the accumulation takes place at a fairly steady rate. It can also perhaps be argued that the ossification of the vertebral epiphyses and the accumulation of corpora lutea could scarcely keep in step with one another in this way except in their relation to the age of the whale, and that therefore the females normally become physically mature at a fixed age in either species after the attainment of sexual maturity (Mackintosh, 1942, p. 221).'

The body length at sexual maturity appears to be a fairly constant proportion of the body length at physical maturity, and has been shown to average 85·1 % (range 80·0–88·5, $\sigma = 3·14$, $I = 3·69$) for a number of cetacean species for which data were available (Laws, 1956*b*). Recent work on pinnipeds confirms that the age at sexual maturity in this group is related to the growth-rate, and it appears that those species which are precocious sexually also show precocious physical maturity (Laws, 1956*b*, 1959*c*). However, it seems unlikely that physical maturity is necessarily attained at a firmly fixed number of years after sexual maturity, but rather that there is a similar spread, as in the age at puberty, over a few years.

Since Wheeler (1930) first demonstrated the correlation between physical maturity and corpora number a large amount of extra material has been collected and it seems worth while briefly to re-examine the relationship.

Material and methods

Wheeler (1930) had data on physical maturity and corpora number from 171 sexually mature female fin whales. In the present material there are 925 sexually mature females for which data on the progress of physical maturity are available, including 642 physically immature females and 283 mature.

This material was accumulated between 1929 and 1949 and I have not included more recent data because the present sample is sufficient to demonstrate the closeness of the correlation. Further material could hardly improve the correlation, but might even increase the variation by adding to the human errors (a further six workers being involved). I am indebted to my colleague Dr R. H. Clarke, who had classified and tabulated this material and who kindly placed his material and a preliminary analysis of the data in my hands.

Some explanation of the procedure followed is desirable. Ideally it would be useful to have for each whale as complete data as possible over the whole length of the vertebral column, but for practical reasons this is impossible. On floating factory ships and to a lesser degree at shore stations there is only a very short period during the working up of the whale (from the time when the meat is removed from the backbone until the vertebrae are sawn up and put into the cookers), when it is possible to examine the vertebral column.

Observers are, therefore, instructed to examine the crucial vertebrae first, namely the fourth and fifth thoracics. If these are unfused they then try the posterior thoracics and if these are still unfused and time permits, then a lumbar vertebra, and if necessary a caudal vertebra, is examined. The rib sockets and chevron bones are useful guides to the different regions. If an epiphysis is unfused a note is made as to whether the cartilage is thick or thin, and if fused, whether the join is visible or invisible. The vertebra is then classed as one of four categories according to the state of fusion—'unfused thick cartilage' (UTC), 'unfused thin cartilage' (UFC), 'fused join visible' (FJV) and 'fused join invisible' (FJI). These categories are illustrated in Text-figure 24. Because the epiphysis has a separate blood supply from the centrum these two parts are sometimes differently coloured, either the epiphysis or the centrum being engorged with blood. This means that the line of fusion can then be picked out even in the fourth class (FJI).

The observations on which this section is based have been made by no less than nine different workers and this naturally results in an increase in the amount of variation. There are two main sources of error: first, in the counts of ovarian corpora, some workers record 'doubtful' corpora much more frequently than others, and the ovaries on which the counts were made were sliced by hand, a method which is likely to lead to small errors of omission. Secondly, and probably more important, are the variations in individual techniques of examining the vertebral column. Attention has already been drawn to the discrepancies between the results of the examination of fin whales by Wheeler (1930) and Peters (1939) on the one hand, and Brinkmann (1948) and Nishiwaki (1950*a*, 1952) on the

other, and as regards humpback whales to the divergence of the results of Chittleborough (1955 b) and Symons and Weston (1958). It is thought that the techniques used by the 'Discovery' Committee and later by the National Institute of Oceanography have been fairly well standardized and that in the present material individual differences in interpretation are reasonably small.

There is, however, a basic cause of variation which must now be mentioned. Fusion of the epiphyses to the centrum progresses from the centre to the periphery (Text-fig. 24) which means that the determination of the state of fusion depends to some extent on the depth at which the line of fusion is examined and is, therefore, influenced by the tools used to examine the vertebrae. When a knife is used the cut is necessarily superficial; with a hand-axe or adze the cut is deeper, but more superficial than the section exposed by use of a felling axe. Other things being equal, the more superficial the examination, the later will be the apparent attainment of physical maturity.
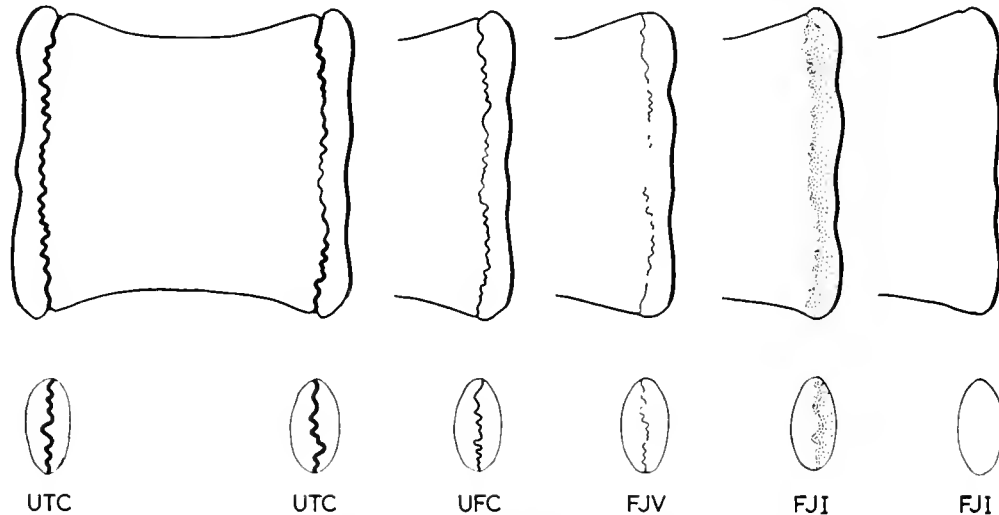
Text-fig. 24. Diagram showing stages of epiphyseal fusion. Above, sagittal section of centrum and epiphysis; below, appearance of tangential chips. The first example of FJI shows how the blood may indicate the line of fusion.

Results

In analysing the data, certain simple conventions have been followed.

(a) As regards the classification of individual vertebrae, fused join visible (FJV) is counted as fully fused. Although the fact that the join is visible means that there is a thin layer of cartilage at the periphery, this layer is not always continuous (e.g. Wheeler, 1930, Pl. V, fig. 2) and usually there is complete fusion in the less superficial parts (Text-fig. 24). Purves and Mountford (1959) have mistakenly assumed this class to be unfused, but have used the figure of 14–15 corpora at the threshold of physical maturity (which is dependent on the FJV classification being classed as fused). Wheeler (1930, pp. 407, 408) also counted FJV as fused. If the FJV group is classed as unfused it naturally raises the threshold of physical maturity in terms of corpora number, as the ovaries associated with Purves and Mountford's ear-plugs show.

(b) Five stages of fusion are recognized. (1) Some or all of caudal vertebrae unfused; lumbar and thoracic vertebrae unfused. (1–2) Caudal vertebrae not seen; thoracic and lumbar vertebrae unfused. (2) Caudal vertebrae fused; some or all lumbar vertebrae fused; thoracic vertebrae unfused. (3) Caudal, lumbar and posterior thoracic vertebrae (11–15) fused; anterior thoracics unfused. (4) Anterior thoracic vertebrae (3–5) fused. The material, classified into these stages, is set out in Table 5.

(c) In classifying the observations in this way it has been assumed first, that if a vertebra is recorded as FJV then the eighth vertebra forward of it will certainly be unfused, and secondly, that if a vertebra is recorded as UTC then the fourth vertebra posterior to it will still be unfused. These assumptions

Table 5. *Progressive stages in the fusion of the vertebral epiphyses in relation to corpora numbers*

Stages of physical maturity

No. of corpora	Immature					Mature	Smoothed	
	1	1–2	2	3	Total	4	Immature	Mature
1	70	29	2	2	103	1	94·0	1·0
2	55	21	—	—	76	—	87·25	0·25
3	53	37	2	2	94	—	78·75	—
4	35	12	4	—	51	—	61·75	—
5	22	17	11	1	51	—	49·25	—
6	20	16	7	1	44	—	47·75	—
7	18	18	12	4	52	—	44·75	0·25
8	6	7	10	8	31	1	33·25	1·0
9	6	3	5	5	19	2	24·5	2·25
10	5	3	13	8	29	4	24·0	3·0
11	4	2	6	7	19	2	22·5	4·25
12	2	3	6	12	23	9	18·5	6·5
13	1	2	1	5	9	6	14·75	6·75
14	—	2	4	12	18	6	13·25	9·75
15	—	1	1	6	8	21	9·5	17·25
16	—	—	—	4	4	20	5·0	19·0
17	—	—	1	3	4	13	3·25	15·75
18	—	—	—	1	1	16	2·0	13·75
19	—	—	—	2	2	10	1·75	13·25
20	—	—	—	2	2	17	1·75	16·25
21	—	—	—	1	1	21	1·0	16·75
22	—	—	—	—	—	8	0·25	12·25
23	—	—	—	—	—	12	—	10·25
24	—	—	—	—	—	9	—	11·0
25	—	—	—	—	—	14	—	11·75
26	—	—	—	—	—	10	—	9·5
27	—	—	—	—	—	4	0·25	7·5
28	—	—	—	1	1	12	0·5	9·25
29	—	—	—	—	—	9	0·25	8·75
30	—	—	—	—	—	5	—	7·25
31	—	—	—	—	—	10	—	8·0
32	—	—	—	—	—	7	—	7·0
33	—	—	—	—	—	4	—	4·0
34	—	—	—	—	—	1	—	3·75
35	—	—	—	—	—	9	—	5·5
36	—	—	—	—	—	3	—	4·75
37	—	—	—	—	—	4	—	4·0
38	—	—	—	—	—	5	—	4·0
39	—	—	—	—	—	2	—	2·25
40	—	—	—	—	—	—	—	0·75
41	—	—	—	—	—	1	—	0·5
42	—	—	—	—	—	—	—	0·5
43	—	—	—	—	—	1	—	0·5
44	—	—	—	—	—	—	—	0·25
45	—	—	—	—	—	—	—	0·5
46	—	—	—	—	—	2	—	1·0
47	—	—	—	—	—	—	—	0·5
48	—	—	—	—	—	—	—	—
49	—	—	—	—	—	—	—	—
50	—	—	—	—	—	—	—	—
51	—	—	—	—	—	—	—	0·25
52	—	—	—	—	—	1	—	0·5
53	—	—	—	—	—	—	—	0·5
54	—	—	—	—	—	1	—	0·5

are based on the condition of the vertebral column in some 23 whales for which fuller records are available, and enable the progress of fusion to be fixed more accurately.

For example, if only lumbar and/or caudal vertebrae are observed and lumbar 10 is FJV then lumbar 2 (eight in advance) is assumed to be unfused, which puts this whale in stage 2. On the other hand, if lumbar 15 is UTC then caudal 4 is assumed to be unfused, thus altering the classification from stage 1–2 to stage 1.

Stages 1–3 are regarded as physically immature, stages 2 and 3 approaching maturity and stage 4 whales are physically mature. It should be noted that this represents the average progress of fusion with completion of linear growth in the anterior thoracic region, but there are a few exceptional whales in which fusion appears to be completed in the middle or posterior thoracic region. It should also be pointed out that the determination of physical maturity is less easy and less certain than the identification of immaturity because the latter is dependent on any one unfused epiphysis, whereas a whale might be classed as stage 4, and therefore mature, although the posterior thoracics were still unfused. However, the good correlation between number of corpora and the attainment of physical maturity suggests that errors are actually small.

Table 6. *Mean lengths of area II females in relation to numbers of corpora*

No. of corpora	Size of sample	Average length	No. of corpora	Size of sample	Average length
1	133	66·9	12	47	73·1
2	107	68·7	13	24	73·2
3	97	69·9	14	29	73·2
4	84	70·6	15	29	72·6
5	69	71·1	16	26	73·0
6	76	72·2	17	24	73·0
7	62	72·0	18	25	72·8
8	51	72·9	19	23	74·2
9	32	72·6	20	21	74·0
10	46	73·1	>20	187	73·0
11	41	72·7	Total	1233	

In Text-fig. 25 a smoothed curve indicating the increase in the mean length at increasing corpora numbers is shown. This is based on 1233 sexually mature females taken in the antarctic area II, that is, presumably from the same stock but over a period of years (Table 6). The mean length at physical maturity in this sample is 73·0 ft. Purves and Mountford (1959) with a smaller sample from area I obtained a figure of 72·9 ft. which is in close agreement.[1] As they point out, their sample may contain a mixture of populations (Brown, 1954), and the present sample is composite in respect of time.

For comparison with this curve of relative linear growth the frequency distributions of corpora numbers at different stages in the progress of epiphysial fusion are also shown in this figure. The 'immature' group includes stage 1 and 1–2; the group 'approaching maturity' is composed of stages 2 and 3, and the physically mature group is stage 4.

The 'immature' group in which, it will be remembered, fusion has not progressed further than the caudal region, corresponds to the period of fastest growth. The average growth is from 66·9 ft. at one corpus luteum or corpus albicans to 72·5 ft. at the mid-point (8·5 corpora) where the 'immature' group overlaps the group 'approaching maturity'. The average amount of subsequent growth to maturity is only 0·5 ft. and is mainly confined to the thoracic region.

In Table 5 and Text-fig. 26 the smoothed frequency distributions of corpora numbers for physically immature (stages 1–3) and physically mature (stage 4) females are drawn. These curves intersect at 14·3 corpora.

[1] Their value for a small area II sample is much higher.

At the overlap there are 31 physically mature females with 14 corpora or less and 23 immature females with 15 corpora or more. Considering these 54 individuals as a normal frequency distribution with a mean value corresponding to the average number of corpora at the threshold of physical maturity, the
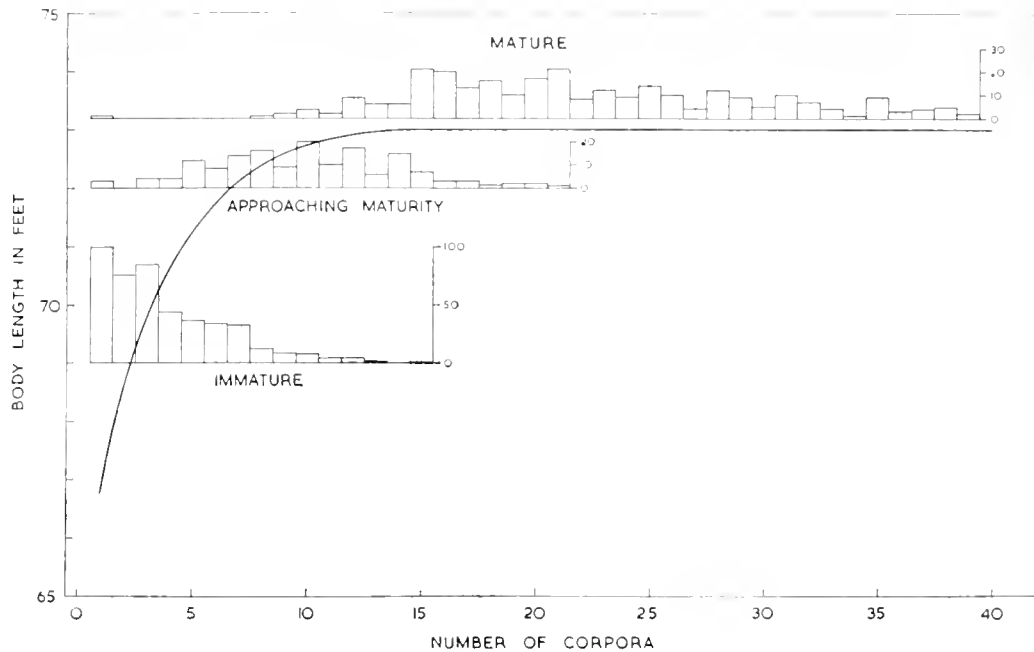
Text-fig. 25. Smoothed curve showing increase in body length with increasing corpora number, together with frequency distributions of corpora numbers at progressive stages of epiphysial fusion.
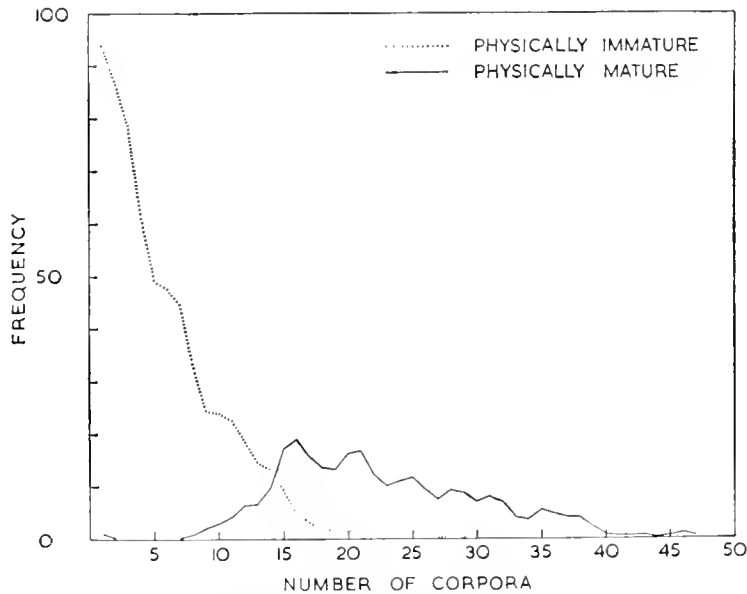
Text-fig. 26. Smoothed frequency distributions of corpora numbers in physically immature and physically mature females.

mean is 14·0 with a standard deviation of 3·94. This is slightly lower than the value at the intersection point (14·3) and is influenced by the effect of mortality on the populations from which the sample is taken. The effect of mortality would be to steepen the right-hand part and to decrease the slope of the left-hand part (as in Text-fig. 27), so that the intersection point is a slightly better indication of the mean number of corpora on the attainment of physical maturity. A further confirmation of the close-

9   D L

ness of the correlation is that, of 53 individuals with 14 or 15 corpora, 26 are physically immature and 27 are mature.

The mean number of corpora at physical maturity is now concluded to be 14·3, and is in close agreement with the findings of Wheeler (1930) and Peters (1939), which were based on smaller samples.

COMPARISONS BETWEEN THE NUMBER OF CORPORA IN YOUNG AGE GROUPS AND AT PHYSICAL MATURITY

In Text-fig. 27 the frequency distributions of corpora numbers at baleen group V (mean number 5·6) and at the threshold of physical maturity (mean number 14·0) are illustrated. For comparison both curves have been converted to percentage frequencies for there is a great discrepancy in the size of the samples. The curves are based on 405 females in baleen group V and only 54 at the threshold of physical maturity. They have been arranged so that the modal number of corpora (5 in the case of baleen group V, and 14·3, the intersect, in the case of the group at physical maturity) corresponds to 0 and the corpora numbers have been converted to values relative to the mode. It is then apparent that the frequency distributions are very similar in shape, the agreement between the right-hand parts of the curves being particularly close. The discrepancy between the left-hand slopes is largely due to the truncation of the group V frequency curve as mentioned above (p. 386). The standard deviations for the curves are 3·30 for group V and 3·94 at physical maturity, and they are in reasonably close agreement. If the two extremes in the frequency at physical maturity (at 1 and 28 corpora) are eliminated the standard deviation becomes 3.00.

We may conclude that the range of variation in corpora numbers at baleen group V is similar to that obtaining at the threshold of physical maturity. It has been suggested that baleen group V includes several year classes and cannot, therefore, represent the range of variation at one specific age, which must be less than this sample shows. Similarly, the group at physical maturity is unlikely to represent a single year class, or even a single age class relative to sexual maturity, but it is not possible to say over how many year classes it is spread and therefore impossible to estimate the probable increase in variation by comparing these two samples.

It would seem to be clear, however, from the small variance at the threshold of physical maturity that there is little variation in the average number accumulated annually by individual whales. In the simplest case linear growth is a decelerating process which begins before sexual maturity and ceases a number of years later. The corpora accumulate annually and the range of variation in the number present at the threshold of physical maturity depends first, on the individual variation in the age at sexual maturity, secondly on the time taken to reach physical maturity and thirdly on the cumulative variation in the annual production of corpora. In this case there can be very little individual variation in the average annual rate of corpora production, because almost all the variation can be accounted for by the age spread at puberty (see below, p. 407). This argument assumes that the accumulation of corpora and ossification of the epiphyses are independent physiological processes. It should be pointed out, however, that oestrogen production (by follicles, corpus luteum and placenta) is associated with each ovulation and pregnancy. One of the biological actions of oestrogens is to delay the ossification of epiphyses in mammals, so that the number of such cycles might well have a direct effect, independent of chronological age, on the attainment of physical maturity. According to this hypothesis females ovulating less frequently than the average would attain physical maturity at an earlier age than those with a higher rate of ovulation, and the frequency distribution of corpora at the attainment of physical maturity might be very similar to that obtained in the present study. If there is such a direct correlation between rate of ovulation and age at maturity then the amount of variation at physical maturity will nevertheless reflect the extent of annual variations between individuals.

Probably neither hypothesis alone is entirely correct and the actual mechanism is likely to be very complicated. In the absence of a sufficiency of marked whales of known age it is unlikely that a satisfactory explanation can be found, but the available evidence suggests that there is a very regular annual increment of corpora in individuals and that the variation in the number of corpora at the threshold of physical maturity is mainly influenced by the spread in the ages at which sexual and physical maturity are attained, and partly by the variation in the annual production of corpora in individuals.
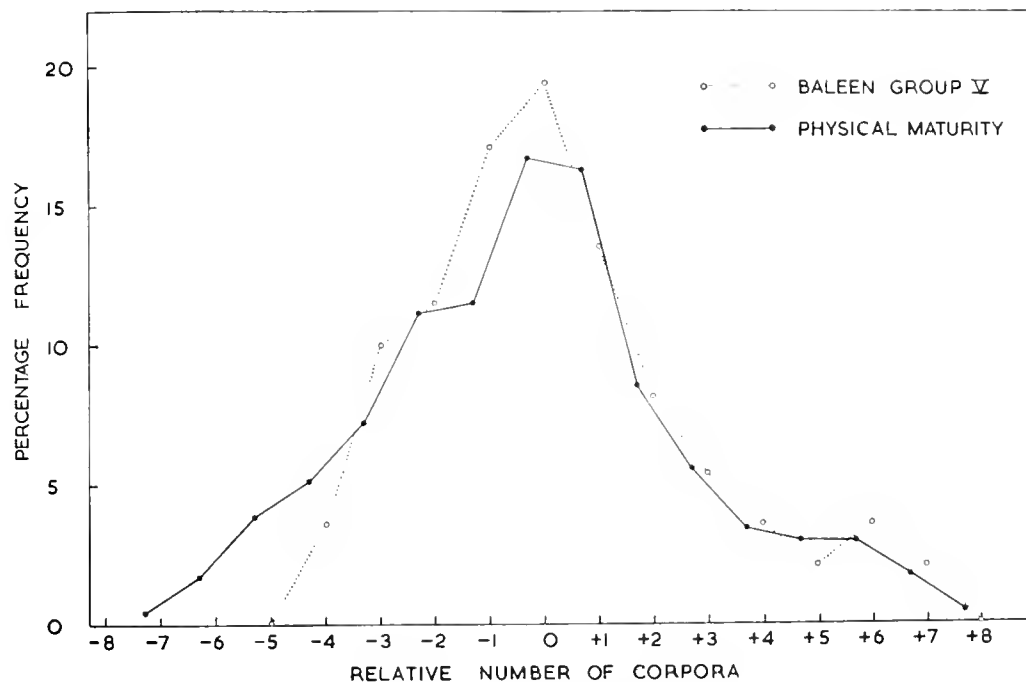
Text-fig. 27. Frequency distribution of corpora at two stages of the life-cycle compared.

The fact that, despite the possible sources of error in the collecting of the data, there is so good a correlation between corpora accumulation and physical maturity points to a rather regular annual rate of accumulation of corpora. This is difficult to account for if the female fin whale is polyoestrous with an average of three ovulations (representing a range of say 1–6 ovulations) per breeding season. This individual variation in the rate of ovulation would alone account for the variance in the number of corpora at physical maturity, without taking account of the age spread at sexual and physical maturity or the possibility of human error. Chittleborough (1955 b, p. 56) presents data which strongly suggest that 'the mean number of ovulations per female humpback during the ovulatory period was only slightly above one'. But if, as seems likely, some two laminations of the ear-plug represent one year (Laws and Purves, 1956; Nishiwaki, 1957; Purves and Mountford, 1959) then the female humpback accumulates about 2·4 corpora on average during each 2-year breeding cycle (Symons and Weston, 1958). That is to say, there is more than one ovulatory period. It has been shown above that newly mature female fin whales, which might be expected to be less successful breeders than multiparous females, have on average only 1·42 ovulations (range 1–4) before becoming pregnant.

In the following sections the reproductive cycle of the fin whale is re-examined in order to find an explanation of the regular rate of ovulation and it is concluded that the female fin whale is probably not polyoestrous as has been assumed by all previous workers. A preliminary announcement of this finding was made in 1956 (Laws, 1956 a).

THE REPRODUCTIVE CYCLE
INTRODUCTION

The framework of the study of the reproductive cycle of the fin whale was laid down by Mackintosh and Wheeler (1929) in their classic work on blue and fin whales, and most of their conclusions still stand. They showed that the season of pairing and parturition extends over a protracted period in the southern winter with a peak in June and July; that pregnancy occupies about 11 months; and that a lactation period of about 7 months was usually followed by a resting period lasting until the next pairing season, so that there is usually only one pregnancy in 2 years. They did, however, note that exceptionally two pregnancies may follow in quick succession as a result of a successful post-partum ovulation in early lactation.

Mackintosh (1942), in summarizing work up to that time, found no reason for altering these initial conclusions as to the interval between pregnancies, but drew attention to a marked increase in the percentage of pregnant females and suggested that this might represent a reaction to whaling. He also stated that there was some evidence that females simultaneously pregnant and lactating were less rare than formerly. He discussed the growth to sexual maturity and concluded that 'while the estimate of two years as the normal period from birth to sexual maturity is not proved, it is unlikely to be more than three years' (p. 225). The evidence on which this conclusion was based was mainly the incidence of unweaned calves and modes in the length frequency distribution of immature whales (Mackintosh and Wheeler, 1929); on the distinction of separate sets of scars indicating migrations in young whales (Wheeler, 1930); and on the recovery of a single female fin whale marked as a calf, which 3 years later was much larger than the mean length at sexual maturity.

This estimate of the average age at sexual maturity was later revised to 3 and then 4 years as a result of age-determinations made on baleen plates (Ruud, 1940, 1945; Nishiwaki, 1952; Hylen et al. 1955) and as a result of the study of the ear-plug to 5–6 years (Purves and Mountford, 1959).

There is now reason to believe that the average age at sexual maturity, although about 5 years in this species is not fixed, but varies slightly with the condition of the stock (Laws, in press) perhaps acting through the food supply. Among wild mammal populations this is perhaps best documented for deer on ranges of differing carrying capacity (Morton and Cheatum, 1946; Cheatum and Severinghaus, 1950). Laws (1956b) has suggested that this may be the result of a higher level of nutrition stimulating bodily growth so that the size threshold for reproduction is reached at an earlier age. It is, therefore, unwise to assume that either the average age or the average length at sexual maturity are unvarying. As regards the length at sexual maturity, Mackintosh (1942) revised slightly the original estimate of Mackintosh and Wheeler (1929) of 65·57 ft. for area II females to 65·24 ft., mainly for samples also from area II. Brinkmann (1948) whose material was also mainly from area II obtained a figure of 65·35 ft. These estimates are all in close agreement. Mackintosh (1942) gave 63·0 ft. as the mean length of male fin whales at sexual maturity.

Mackintosh (1942) discussed the important question as to whether whales are monoestrous or polyoestrous. He concluded that ovulation is spontaneous and that, although the evidence is not conclusive, it strongly suggests that whales are polyoestrous. He remarks: 'If it were found, contrary to expectation, that whales were in fact monoestrous, the determination of age from corpora lutea numbers would of course be enormously simplified' (p. 222).

Chittleborough's (1955b) data on the humpback whale suggest that in the great majority of individuals there is only one ovulation during the ovulatory period, but that this is a case of later polyoestrous cycles being suppressed because the first ovulation is successful, so that it is effectively monoestrous. However, there is evidence (p. 393) that in the humpback whale there are on average

probably two to three ovulations per 2-year cycle, which means, if correct, that there must usually be more than one ovulatory period in the course of the 2-year cycle. Chittleborough is the only worker who has been able to carry out extensive studies on a large whalebone whale in low latitudes during the winter, that is near the breeding grounds during the breeding season. His direct observations confirm the inferences about the breeding season and gestation period of humpback whales made from records of foetal lengths (e.g. Matthews, 1937). This is encouraging and suggests that such an approach should give fairly accurate results for other species (Laws, 1959a).

It has been necessary in parts of the following account to draw analogies with other mammals, but owing to the practical difficulties of verifying such points as, for example, the duration of the corpus luteum of the cycle in the whale, this approach is unavoidable.

THE SEX RATIO

Mackintosh (1942, tables 21 and 22) gives records of the sex of 13,379 fin-whale foetuses and 119,385 post-natal fin whales. The foetal records show a significant difference in the proportions of the sexes (52·0% male, S.E. of the percentage 0·19), and the other records show an even greater preponderance of males (54·5%, S.E. of the percentage 0·02).

. The interpretation of the second figure is difficult. Lactating females are under-represented on the antarctic whaling grounds and, as their taking has been prohibited for many years, even less well represented in the catch. Conversely, there has probably been some selection by the whalers of females because of their larger size, and the minimum size limits give greater protection to the males (see Laws, 1960). Mackintosh (1942, p. 267) concludes that there are slightly more males than females.

THE BREEDING SEASON

The breeding season is here defined as the period of pairing and parturition. Since pregnancy extends over almost a year these two activities take place at the same season of the year. It is clear from the wide variation in foetal lengths in any one month that it is a protracted period. In fact, conceptions occur and calves may be born in almost every month of the year, but most of this activity is confined to a relatively short period. There are several methods by which we can obtain an estimate of the monthly frequency of pairing.

The male reproductive cycle

The mating season depends to some extent on the cycle of activity of the males. Thus if, in the male, rut is short and well-marked, the season of pairing will probably also be well-defined and the season of parturition limited. This relationship is very clear in the pinnipedia, in some of which the pairing season is confined to two months or less (Laws 1956c).

In investigating the male reproductive cycle of fin whales little direct evidence is available because of the inaccessibility of the breeding population and we must resort to indirect methods (as in the case of females).

Histological evidence

One method is to attempt to distinguish a cycle of activity in the gonads, but here again there are difficulties. A point which has not perhaps been sufficiently emphasized by previous workers is that the epithelium of the seminiferous tubules is more sensitive to post-mortem changes than most other tissues. These changes often take the form of extensive desquamation, of at least the superficial layers, which is similar to natural and experimentally induced testis degeneration.

In most pelagically caught animals the time from death to the examination is about 5–10 hr. and

whales under 3 hr. post-mortem are rare on factory ships or land stations. The insulating layer of blubber probably accelerates post-mortem changes. Chittleborough has studied the histology of humpback-whale testes from animals in breeding condition, but the material shows signs of post-mortem degenerative changes, with the result that even his material does not present a clear picture of full spermatogenesis (Chittleborough, 1955 b, Pl. 1, fig. 4). In most cases it has been found possible to diagnose a male in full breeding condition or in complete anoestrus, but it is not possible to describe the more gradual histological changes accompanying the approach to or regression from full breeding activity as was possible with well-fixed material collected from seals immediately after death (Laws, 1956 c). A preliminary examination is sufficient to show that most male fin whales examined in the
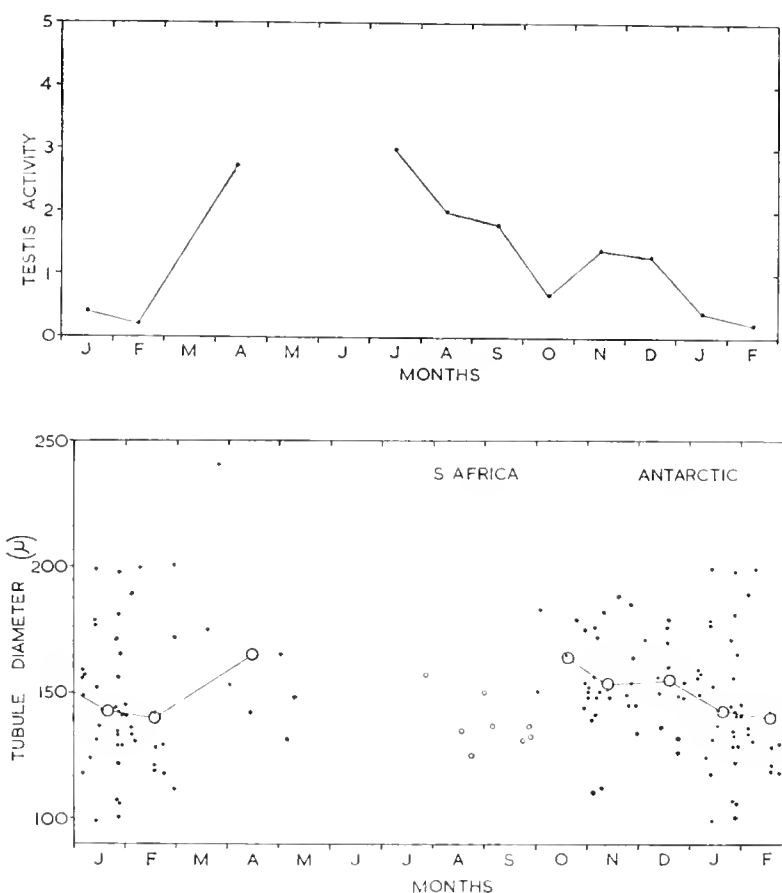
Text-fig. 28. Annual cycle of testis activity in the male. Above, activity expressed as arbitrary scale of values, based on histological appearance; below, measurements of mean diameters of seminiferous tubules; from Antarctic and South Africa.

Antarctic are in full anoestrus, but there are some individuals in which the seminiferous tubules present a more active picture.

Since detailed histological examination and description is not rewarding, a subjective classification into five arbitrary stages of activity has been made using the sectioned material on which Mackintosh and Wheeler (1929) based their account of the male cycle. This includes 86 specimens, mostly from January and February, but including all months except June. On the basis of the overall microscopic appearance the material has been divided into five classes—0, 1, 2, 3 and 4, ranging from complete anoestrus to full activity. The monthly mean according to this scale of values has been calculated and the results are set out in Table 7 and Text-fig. 28. Almost all the pelagic material collected in recent years is from January and February and the great majority of specimens fall into group 0 as in the earlier material; it has not, therefore, been included.

Smears of testes and epididymides from 17 mature fin whales were examined by A. H. Laurie and F. D. Ommanney at Durban, South Africa (unpublished work). This material was collected in June, July and August and spermatozoa were present in all except two specimens.

Table 7. *Arbitrary classification of testis samples according to activity*

| Month | Sample size | Arbitrary classification | | | | | Arbitrary mean |
		0	1	2	3	4	
January	21	16	3	—	2	—	0·4
February	35	33	—	—	2	—	0·2
March	2	—	1	—	1	—	2·0 ⎫
April	4	—	—	3	1	—	2·2 ⎬ 2·8
May	3	—	—	—	—	3	4·0 ⎭
June	—	—	—	—	—	—	—
July	1	—	—	—	1	—	3·0
August	4	—	—	4	—	—	2·0
September	5	—	2	2	1	—	1·8
October	3	1	2	—	—	—	0·7
November	5	—	3	2	—	—	1·4
December	3	—	2	1	—	—	1·3
Total	86	50	13	12	8	3	—

From this examination it appears that the period of maximum testicular activity extends from about April to July or August with peak activity probably in May and June, and it is at a minimum in January and February. Owing to the scarcity of material from March to October it is not possible to say more than this.

Variations in the diameter of the seminiferous tubules

Individuals of many species of mammals show a seasonal cycle in the diameter of the seminiferous tubules, correlated with histological changes in the contents of the tubules (Laws, 1956c). The seminiferous tubules are narrow in anoestrus, enlarge just before the breeding season and shrink again afterwards. Whales might be expected to show a similar cycle of growth and regression, but the full extent of these changes appears to be masked by the amount of chronological variation in the individual cycles. Chittleborough (1955a) for instance, could demonstrate no change in testis weight or in the diameter of the seminiferous tubules of humpback whales taken over a period of 4½ months from June to October, but Omura (1953) and Symons and Weston (1958) found the testis weight to be lower in antarctic specimens than those in Chittleborough's sample. These authors also state that the testes of humpback whales taken in February present an inactive appearance when examined histologically.

As explained above, whale testis material is often badly fixed and shows degenerative changes. In measuring the diameter of the seminiferous tubules only material which showed no obvious shrinkage of the tubules has been accepted. This limits the material to samples from 95 mature male fin whales, the histological appearance of the tubule contents being the criterion of maturity adopted. As the testis of males approaching puberty probably presents an appearance similar to that in inactive mature males, it is possible that some immature males have been included inadvertently, but these are unlikely to have much effect on the general conclusions.

For each of these 95 whales the mean tubule diameter was calculated from a random sample of 20 tubules, except for a small minority in which only 10–15 were measured. Measurements were made with a graduated scale on projected histological sections and only roughly circular tubule sections were measured across two diameters at right angles; this helped to make the samples random and ensured that the full tubule diameter was measured.

Table 8. *Summary of records of the diameter of seminiferous tubules of antarctic male fin whales by months*

Month	Mean diameter (μ)	Range (μ)	Sample size
October	164	144–183	7
November	154	110–188	22
December	155	126–179	13
January	143	99–199	30
February	140	112–200	16
March ⎫ April ⎬ May ⎭	165	131–241	7

The results are shown in Text-figs. 28 and 29 and summarized in Table 8. Taking first the antarctic samples it will be seen that, although there is a wide range of variation in tubule diameters, the monthly mean value progressively declines from 164 μ in October to 140 μ in February. This continued decrease in the tubule diameter strongly suggests that the testes of male fin whales taken in the Antarctic from October to February are regressing following a season of activity at an earlier period. Clarke (1956) found a closely similar decrease in monthly mean tubule diameters in male sperm whales taken in the vicinity of the Azores (from 161 μ in June to 134 μ in September and 144 μ in October).

After February there is apparently an increase in the tubule diameters. The monthly mean for March is 208 μ, but this is probably too high, being the average of only two whales, and probably over-influenced by the high value for one of them (tubule diameter 241 μ, the largest tubule diameter measured). The lower of these two values (tubule diameter 175 μ) was from a specimen in which the tubules were in early spermatogenesis and, therefore, probably enlarging prior to the breeding season. The other specimen had a number of degenerating spermatids in the lumen and may have been either approaching rut, or immediately post-rut. An observation of the extent of diatom infection might have helped to place this very interesting animal (see below), but unfortunately no notes were made on this point in the field. If the seven specimens for March, April, and May are taken together they suggest a mean diameter of about 165 μ in April.

Turning now to the testis tubule diameters for the eight mature males from Saldanha Bay, South Africa, taken in July, August and September (Text-fig. 28) it will be observed that only two have tubules above 140 μ in diameter, which is very much lower than expected. These few specimens suggest a possible decline in tubule diameter over this period but the August and September means are below the lowest monthly mean values in the antarctic samples. Referring again to the arbitrary scale of testis activity based on the histological appearance of the seminiferous epithelium it will be seen that these testes from July, August, and September are more active than those from later months. The most probable explanation of the discrepancy is that the post-mortem and post-fixation treatment has been different, and has produced greater shrinkage in the South African material. It will, however, be remembered that only fin-whale material showing no obvious shrinkage has been used. It is relevant to note that the frequency distribution of humpback-whale tubule diameters, measured by Chittleborough (1955a, fig. 10), is almost the same as that for fin whales. These are compared in Text-fig. 29 A and C, and it will be noticed that two fin-whale values are higher than the highest value for humpback whales. The present material was Bouin-fixed or formol-saline fixed whereas Chittleborough's material was fixed in Susa or formol-saline. The different fixation should not in itself produce very marked differences in shrinkage, and most shrinkage occurs in pre-embedding preparations (Baker, 1958). Symons and Weston (1958) also give a mean tubule diameter for a sample of

eleven humpback whales taken in February which is higher than that for Chittleborough's sample. In fact the maximum diameter they found was 290 μ which seems very high, but their sections were cut from frozen material without embedding, so the shrinkage would be expected to be much less than in paraffin-embedded material. We are comparing here anoestrous fin and humpback whales with humpback whales in rut and one would expect the latter to show much higher values with identical treatment.

In pinnipeds of at least four widely different genera the tubule diameters in rut are about 220 μ and shrink to less than 140 μ in anoestrus (Laws, 1956c, fig. 7; McLaren, 1958, fig. 3; Mansfield, 1958, fig. 15). The antarctic fin-whale material suggests that there is a similar range in whales. In this material anoestrous tubules are about 140 μ in diameter (Text-fig. 28) and the largest measured (241 μ) was either approaching rut or taken immediately after.
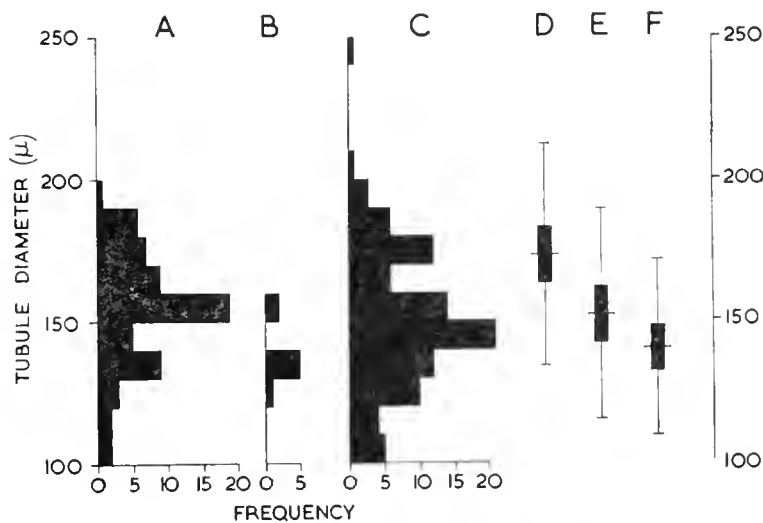
Text-fig. 29. Measurements of seminiferous tubules. A, humpback whale, West Australia; B, fin whale, South Africa; C, fin whale, antarctic; D, E, and F, means $\pm 2\sigma$ and s.e. for antarctic fin whales classified as to diatom infection; D, recent arrivals; E, heavy diatom infection, South Georgia; F, heavy infection, antarctic pelagic.

It seems probable then that the fin-whale material from South Africa and the humpback-whale material from Australia has undergone much greater shrinkage than the antarctic material, so that the testis tubule diameters cannot be directly compared. It is also possible, however, that the South African material gives a true picture, relative to the antarctic material, and that there is a decrease in average tubule diameter from July to September, followed by an enlargement associated with the southward migration. This possibility is discussed later (p. 453). It seems clear, when the evidence is combined, that there is a very definite cycle of activity in the male fin whale. It should be noted that the bulk of the fin-whale population is in the Antarctic during the months covered by the samples because at this time they must feed in antarctic waters (Mackintosh and Brown, 1956, fig. 2; Marr, 1956). It can safely be assumed that, so far as it goes, the material gives a true picture of the male sexual cycle.

The individual rate of regression in tubule diameter is actually greater than Text-fig. 28 suggests, because of the smoothing effect of the continued arrival in the Antarctic of males from lower latitudes. Even in January and February there are some males with seminiferous tubules about 200 μ in mean diameter and it seems likely that these are recent arrivals. Is there any way of confirming this? Hart (1935) showed that the presence of a thick diatom film on the surface of the body can be taken to indicate that a whale has been in antarctic waters for at least a month, and conversely, the absence

of a diatom film or the presence only of small patches on the jaw is characteristic of whales which have only recently entered the colder waters.

Records of both the extent and heaviness of diatom infection and of the mean diameter of the seminiferous tubules, are available for a number of fin whales from South Georgia and the pelagic whaling grounds. When doubtful cases have been eliminated the sample for which precise information is available is reduced to only 43 male fin whales.

Table 9. *Summary of information on the diameters of the testis tubules of 43 male fin whales classified by means of diatom infection*

| | | Heavy diatom | |
	Recent arrivals	South Georgia	Pelagic
Sample size	13	14	16
Mean diameter (μ)	173	152	140
Range	(149–201)	(127–183)	(119–171)
σ	19·73	18·64	15·40
S.E.	5·20	4·98	3·85

For 13 recent arrivals with little or no diatom infection, the mean tubule diameter is 173 μ; for fourteen whales taken at South Georgia with heavy diatom infection which had, therefore, been in the Antarctic for several weeks the mean tubule diameter is 152 μ. For 16 with heavy diatom infection, taken pelagically much further south, which had presumably been in colder water even longer than the last group, the mean tubule diameter is 140 μ. There is a similar range of variation in all three samples (Table 9), suggesting that the rate of regression is fairly constant.

These mean values plus or minus 2σ and 2 S.E. are shown in Table 9 and Text-fig. 29 D–F, and it will be seen that the mean values for the tubule diameter in recent arrivals and in animals which have been south of the antarctic convergence for some time are significantly different. These values may be compared in the same figure with the frequencies of tubule diameters in the larger unclassified sample (Text-fig. 29 C). There are two modes in this frequency distribution, the higher of which is now seen to correspond to recent arrivals in the Antarctic in which the tubules are still shrinking, and the lower mode represents males in which the tubules are almost fully regressed. The mean diameter of fully regressed tubules in mature fin whales is probably about 140 μ, for material fixed and embedded in this way. The last phrase is an important qualification.

These results may be compared with the mean diameter of the testis tubules of 13 immature fin whales, which is 79 μ (range 47–113 μ). This is almost identical with the findings of Chittleborough (1955a) for the humpback whale and close to the figures given by Clarke (1956) for the sperm whale. One specimen, taken in October, which appears to be approaching puberty has a mean tubule diameter of 102 μ (open tubules 122 μ; closed 82 μ), which is again close to Chittleborough's figures. It is difficult to reconcile this with the apparent extensive shrinkage of the tubules of mature humpback whales in rut, but whether this shrinkage is postulated or not, it does not affect the general conclusions given below.

This brief discussion of testis histology is sufficient to establish that there is an annual cycle of testis activity in the male fin whale. The season when the majority are in active spermatogenesis probably extends over the period April–September, with most activity in April, May, June and July. It is in these months that the majority of conceptions should occur. Nevertheless, the presence of some males in January, February and March which have testis tubules up to 200 μ in diameter suggests that successful pairings can occur in almost any month.

The follicular cycle in females

The cycle of follicular activity in female fin whales has been discussed in an earlier section of this paper. In adult females there are usually large numbers of resting or regressing follicles, often of large size, and this makes any attempt to demonstrate a cycle of follicular activity difficult owing to the limited period for which data are available.

This difficulty can be overcome by considering only the size of the largest follicle in fin whale females approaching puberty. In the present material there are 62 pairs of ovaries from immature females at this stage of the life-cycle, and the results obtained were described on pp. 346–47, Table 2, and Text-fig. 3. It was concluded that immature females ovulate for the first time between June and November (possibly also December) and that from January to May the ovarian activity is at a minimum. It will be shown (p. 411) that the annual cycle of immature females is retarded relative to that of mature females and this evidence, therefore, supports the inferences about the season of pairing drawn from evidence from the male cycle and from a consideration of foetal lengths (see below).

Pregnancy and foetal growth

If the rate of foetal growth is known with reasonable accuracy then it should be possible to obtain an estimate of the frequency distribution of pairings and conceptions by examining the foetal length records, as was done by Mackintosh and Wheeler (1929, pp. 426–7) for blue and fin whales. However, small errors in the estimated curve of foetal growth can lead to quite large errors in the calculation of the frequency distribution of conceptions. For this reason it is necessary to obtain an average curve of foetal growth which is reasonably accurate, before going on to use this to determine the monthly frequency of pairing. It is also necessary to show to what extent the length frequencies of foetuses in the sample examined may be taken to be representative of the foetal length frequencies in the population sampled, and the extent of the differences, if any.

In a recent paper (1959a) I reviewed earlier work on the problem and went on to examine the rates of foetal growth in three Odontocete species and five Balaenopterids. The material for the fin whale included length records of 956 foetuses from South Africa (5), South Georgia (268) and from the pelagic whaling grounds (683). I found that the method developed by Huggett and Widdas (1951) for dealing with foetal length and weight data appears to hold good for the Odontocete species studied and to a limited extent for the Balaenopterid species. In particular this method provides for an objective estimate of the length of the initial period of very slow growth (before the placental circulation is fully established?) which is impossible by means of freehand extrapolation. In the Balaenopterid species growth after this initial period is linear as in the Odontocetes, but unlike this group, the phase of linear growth appears to be superseded by a phase of exponential growth in the second half of pregnancy. My (1959a) conclusions about foetal growth in length in the fin whale are presented and summarized in Table 10 and Text-fig. 30, and the original paper should be consulted for further details. The average duration of gestation in this species is estimated to be $11\frac{1}{4}$ months (early June to mid-May). This evidence of the mean date of pairing agrees very well with the evidence from the male sexual cycle and reasonably well with the ovarian cycle in females approaching puberty. It is shown below (p. 411) that the beginning of pregnancy in primiparous females is later than the average date of conception in multiparous females.

The explanation of the relatively large variation in the foetal lengths in the monthly samples is undoubtedly that the pairing season both for primiparous females and multiparous females extends over several months, as will be shown below.

The frequency distributions of foetal lengths in the monthly samples were examined in the above

paper (Laws, 1959a) and it was shown that the samples taken in the Antarctic in the period of 5 months from October to February may be considered to be representative of the progress of foetal growth, but that differential migration out of the area affects the validity of the samples from March onwards. A similar differential migration into the area in spring means that very early embryos (less than one month post-conception) will tend to be absent in antarctic samples. The effect of this would be most marked in the earlier months, prior to November, for which in any case very few length records are available.

It is estimated that, in addition to the 956 foetuses recorded in Table 10, little more than 50 (some 5%) would have to be added to the lower size groups of the frequency distributions for October and
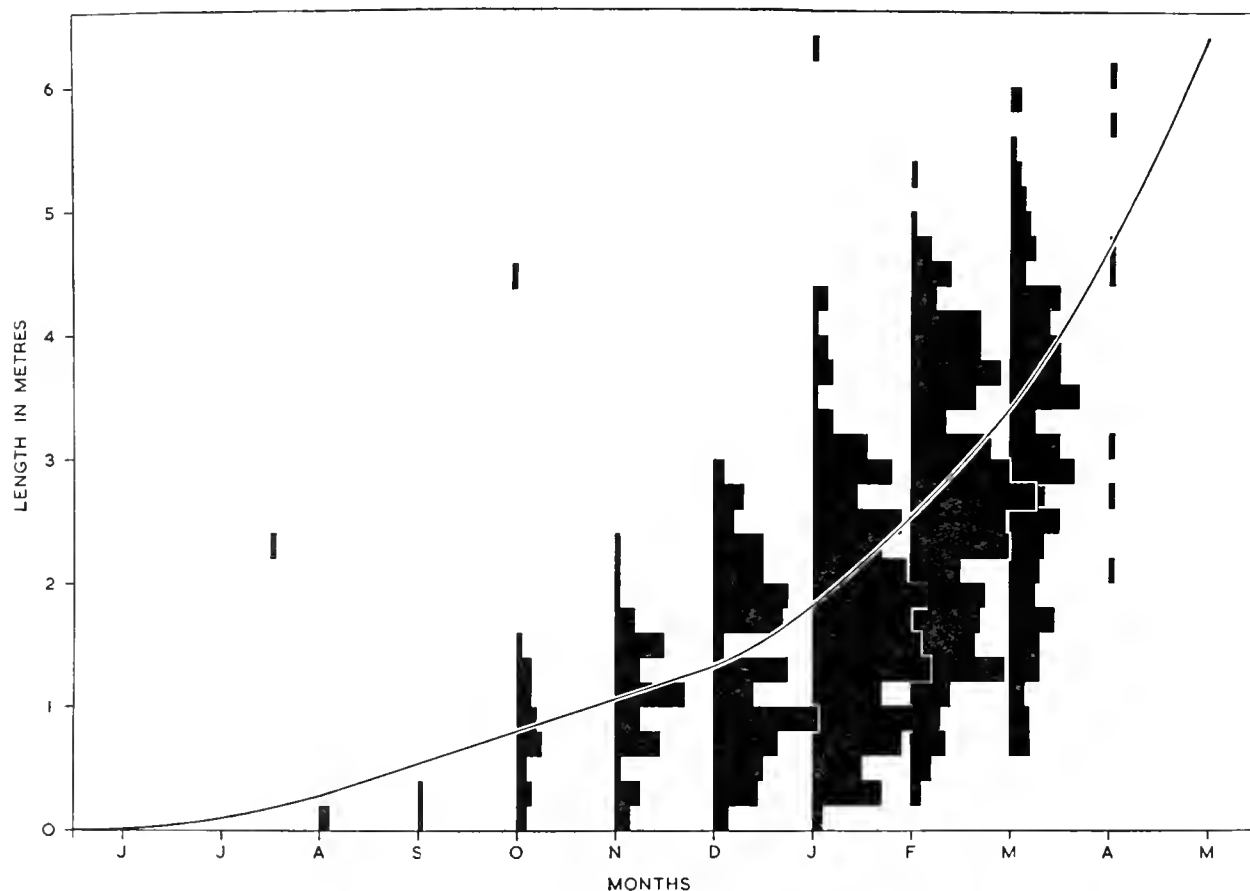
Text-fig. 30. Mean curve of foetal growth and monthly foetal length frequencies of southern hemisphere fin whales; class interval 0·2 m.

November, and the higher size groups of the March and April samples, to overcome this bias. The effect of this small error on the frequency distribution of pairing, which is now to be calculated, means that the pairing frequencies for the early months of the breeding season and for the late months will be slightly under-represented. This is thought to have a negligible effect on the shape of the pairing curve.

The effect of individual variation in growth-rates must also be considered. Zemskiy (1950a) states that male and female foetuses grow at different rates. Kimura (1957, p. 113) studied the difference in length between twins of different sexes, but found that in 57% of cases there was no difference, and the remainder were almost equally divided between pairs in which the female was larger and pairs in which the male was larger. No distinction as to sex need, therefore, be made in studying foetal growth. We are concerned here with the average growth of large numbers, so individual variations in the growth-rate need not be considered in drawing up an average growth curve. When foetal lengths are

Table 10. *Growth in length of southern hemisphere fin-whale embryos*

Month	Size of sample	Mean length (m.)	2 S.E.	Fitted curve
12 June	—	—	—	0·00
Mid-July	—	—	—	0·10
Mid-August	3	—	—	0·30
Mid-September	2	—	—	0·55
Mid-October	23	0·809	0·158	0·80
Mid-November	59	1·069	0·128	1·07
Mid-December	142	1·377	0·121	1·33
Mid-January	271	1·775	0·112	1·82
Mid-February	284	2·620	0·128	2·55
Mid-March	165	3·056	0·188	3·40
Mid-April	7	4·128	1·154	4·70
Mid-May	—	—	—	6·40
Total	956	—	—	—

used to determine the pairing season, individual variations will have the effect of slightly extending it. It should be noted that this effect tends to cancel out the effect produced by the under-representation of very small embryos and very large foetuses in the sample.

It has now been shown that, for the purpose of establishing the frequency of conceptions in the fin whale, the foetuses for which data are available (956 in number) may be taken to be a representative sample. For the reasons given above any errors are likely to be small.

The pairing season and the season of parturition

The evidence which has been considered above strongly suggests that the majority of pairings in the southern hemisphere fin whale take place during the period April–July. It is now possible to obtain a more precise idea of the relative frequency of pairing by examining the foetal length data, using the method employed by Mackintosh and Wheeler (1929, p. 427, fig. 146).

First, the 956 foetal lengths were plotted according to the dates on which they were taken. The mean curve of growth in foetal length (Table 10, Text-fig. 30) was then drawn and similar curves constructed at lateral intervals of one month. The foetuses which lie between two of these growth curves can then be referred to the monthly periods in which they were conceived. The effect on the results of uneven sampling and individual variation in the rate of growth have already been discussed (p. 402) and it was concluded that these influences tended to neutralize each other.

All the foetal length records have been referred to the various monthly periods of conception, for example 12 June–11 July, and the frequency distribution of conceptions, determined in this way, is shown in Table 11. The actual frequencies have been converted to percentage frequencies and are plotted graphically in Text-fig. 31. It will be seen that although 12 June is estimated to be the mean date of conception, the distribution of pairings about this mean date is not symmetrical, but skewed, so that the modal frequency occurs earlier than the mean. This curve of the frequency of pairing is in close agreement with the conclusions reached from consideration of the male sexual cycle, and of the ovarian cycle of females near puberty. It is estimated that 77% of foetuses are conceived in the 4 monthly periods between April and August; only about 14% of all foetuses are conceived in the 7 monthly periods from September to April, and only about 6% in the 5 months between October and March. This demonstrates that there is a limited season in the female extending over 4–5 months during which most conceptions occur, but it will be noted that some foetuses may be conceived in every month of the year except February.

It has already been shown that the duration of the gestation period is about $11\frac{1}{4}$ months. A curve showing the seasonal distribution of calving has, therefore, been constructed by advancing the curve of conceptions by 3 weeks (Text-fig. 31).

So far we have been concerned with the pairing season averaged from data collected over a number of years. It would be interesting to know the possible variation in the timing of the pairing season from year to year.
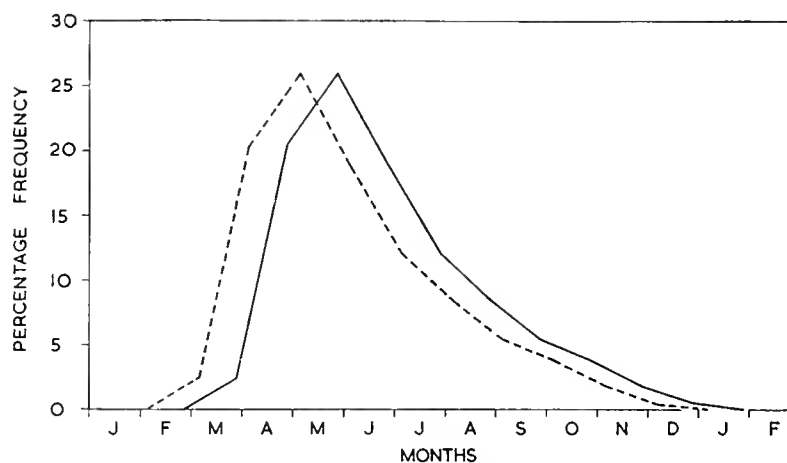
Text-fig. 31. Monthly percentage frequency of pairing (full line) and calving (broken line) of 956 pregnant females.

Table 11. *Estimated frequency of conceptions in southern hemisphere fin whales, based on 956 records of foetal length*

	Conceptions	
Monthly period	*No.*	*Percentage*
January/February	0	0
February/March	1	0·1
March/April	23	2·4
April/May	196	20·5
May/June	249	26·0
June/July	180	18·8
July/August	116	12·1
August/September	81	8·5
September/October	52	5·4
October/November	36	3·8
November/December	17	1·8
December/January	5	0·5
Total	956	99·9

Our material collected by biologists is inadequate for this purpose, but there is information on foetal lengths of fin whales in the International Whaling Statistics covering the period 1925–58 and comprising many thousands of records. These measurements are not as accurate as those made by biologists which were used to elucidate the curve of foetal growth and the average pairing season. As Brinkmann (1948) has pointed out, small foetuses tend to be missed so that in the earlier months the mean foetal lengths given in the International Whaling Statistics are higher than expected in a true sample. However, we are interested in relative differences from year to year and the absolute lengths are not important in this connexion.

In Text-fig. 32 the mean monthly foetal lengths given in the International Whaling Statistics have been converted from feet to metres, and are plotted against the respective whaling seasons. The records

for 1925–30 are averaged and there is a gap between 1940 and 1945 corresponding to the reduced whaling activity during the war. Only 4 months (December–March) are considered, because the samples from other months are small, and no mean value is given for December 1932 because there were only eight individuals in this sample. From 1934 onwards the samples are large (usually from a hundred to over a thousand).

It will be seen that in the three decades covered by the material there has been no significant progressive change in the mean monthly foetal lengths for December and January. The values for March and perhaps February suggest that the rate of foetal growth may have increased slightly. There have, however, been variations from year to year, although the pattern of the curves for the different months is not always the same, indicating that some of these variations are not significant. There are seasons when monthly mean foetal lengths deviate significantly from the monthly mean for the whole
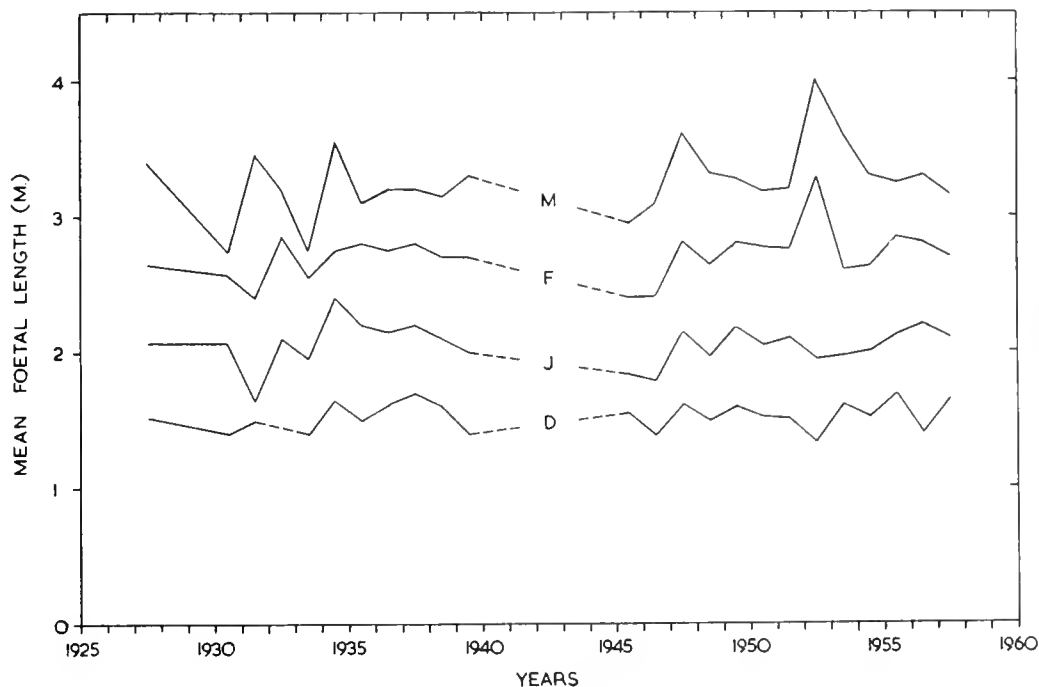
Text-fig. 32. Variation in the mean monthly foetal lengths over the period 1925–58 (from International Whaling Statistics, Sandefjord).

period. In January 1935 and February 1953 for instance, where there is a large deviation from the overall mean for the period, the calculation of the mean ± 2 S.E. shows that these particular values deviate significantly by more than 0·25 m. and about 0·5 m. respectively, from the means for the full period.

Deviations of this order could represent displacements of the mean date of conception of about 1–2½ weeks (from Text-fig. 30), but a number of complicating factors need to be considered in assessing this temporal deviation. Have there, for instance, been any changes during this 30-year period in the rates of foetal growth? Have changes in the age structure of the populations of mature females been sufficient to produce an apparent change in the pairing season? It is not possible to provide conclusive answers to these questions, but such changes would probably be progressive and would not account for variations from year to year. It may be that a slight increase in the rate of foetal growth, and a shift towards lower ages in the age structure of the mature females, could produce an apparent advancement or retardation of the pairing season.

On the evidence available it seems probable that there has been no progressive change in the pairing

season, and that annual variations in the mean date of pairing have been within the extreme range of $\pm 2\frac{1}{2}$ weeks, during the period for which data are available. It is possible that variations in the spatial distribution of the catches are partly responsible for these fluctuations, that is to say, the timing of the pairing season or the foetal growth-rate may be slightly different in the different oceans, but it seems more likely that climatic factors are at work. A year when pack-ice was late in retreating might retard the southward and northward migrations and delay the pairing season. Dawbin (1956) has shown that at Cook Strait, New Zealand, the mid-point of the northward migration of humpback whales is 5 July. In 36 seasons the maximum variation has been from 21 June to 29 July, that is about 5 weeks. This is in quite close agreement with the conclusions about the annual variations in the monthly mean sizes of fin-whale foetuses. It is a problem which might well repay further study.

Sexual maturity

Strictly speaking the term sexual maturity should be applied to the peak period of reproductive performance when fertility and reproductive rate are at a maximum. In the literature on whales the attainment of sexual maturity is understood to refer to that part of the life-cycle when females first ovulate and males first produce sperm. Although it thus corresponds more accurately to puberty, because of its wide use the term sexual maturity is retained here, although it is not strictly correct.

The mean length at sexual maturity

Various estimates of the length at the attainment of maturity of female southern hemisphere fin whales have been made, all of which correspond rather closely. Mackintosh and Wheeler (1929) estimated the mean length of the female at sexual maturity to be 65 ft. 7 in. This was later amended by Mackintosh (1942) to 65 ft. 3 in., using the same data as well as additional records accumulated up to 1941. Brinkmann (1948) concluded that the mean length at sexual maturity is 65–66 ft.

Estimates of the mean length of the female at sexual maturity made by Japanese workers range from 67 to 68 ft. (Nishiwaki, 1950; Nishiwaki and Hayashi, 1950; Nishiwaki and Oye, 1951), but the figure of 64 ft. given by Nishiwaki (1957, p. 30) does not agree with these earlier estimates. The apparent discrepancy between the results of Japanese and European workers is accounted for by the fact that the former take the average length at sexual maturity as the length when 75% of females are sexually mature. (Their reasons for this procedure are not clear.) When recalculated by taking the length at which 50% are mature and 50% immature, the mean length is seen to be about 65 ft. (Nishiwaki, 1950, fig. 22 b) and conforms closely with the other estimates obtained in this way. The European material is mainly from antarctic areas II and III, whereas the Japanese material is mainly

Table 12. *Length frequencies of sexually immature and mature fin whale females*

Length (ft.)	Immature	Mature
60	50	3
61	40	1
62	52	9
63	56	8
64	45	20
65	60	39
66	33	64
67	19	65
68	20	98
69	11	137
70	1	143
71	2	169
Total	389	756

from area V. This close agreement between material from different areas of the Antarctic is particularly interesting in view of the much lower size at sexual maturity of northern hemisphere fin whales (Jonsgård, 1952; Pike, 1953) and the reported difference between the lengths at maturity of this species in the North Pacific and in the East China Sea (Miyazaki, 1958); also in antarctic areas I and II (Purves and Mountford, 1959).

The question of the mean length of the female fin whale at sexual maturity has been re-examined using the material available to Mackintosh (1942) and in addition several hundred observations made up to 1954 on behalf of the 'Discovery' Committee and the National Institute of Oceanography. This new material increases the number of records of immature and mature females between 60 and 71 ft. from 402 to 1145. The data are presented in Table 12. In Text-fig. 33 these length frequencies, smoothed by threes, are shown and it will be seen that the intersection of the curves for sexually immature and mature females is at 65·25 ft. There are 80 sexually mature females below the intersection point and 86 sexually immature females above. Taking the lengths of these 166 individuals
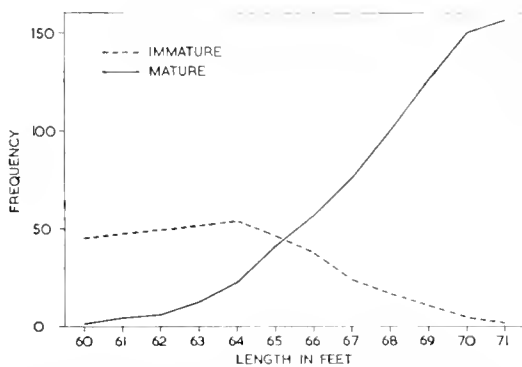
Text-fig. 33. Smoothed length frequencies of sexually immature and sexually mature females.
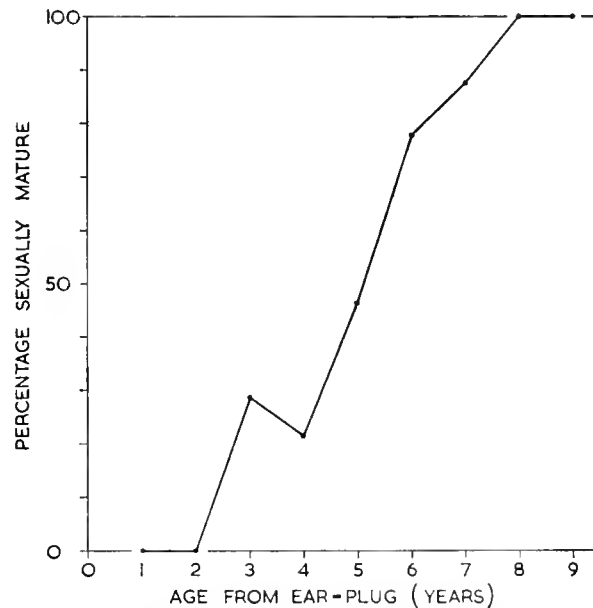
Text-fig. 34. Percentage of sexually mature females in successive age groups.

as a normal frequency distribution with a mean value corresponding to the average length at puberty, the mean is 65·41 ft. (standard deviation 2·07, standard error 0·16). This is in close agreement with the value of the intersection point of the curves. The mean length at puberty is therefore taken to be 65·25 ft. The larger sample has extended the range of overlap by a few feet from 61–69 to 60–71 ft., but the mean length at sexual maturity remains identical with the earlier estimate of Mackintosh. It should be remembered that this mean length is derived from material representing several areas.

The diagnosis of sexually mature males is not so easy, nor so precise. It depends either on histological criteria or on consideration of the size of the testis. The estimate given by Mackintosh (1942) is based on 770 sexually immature and mature males up to 69 ft. in length, and his figure of 63 ft. is accepted here, because the new material did not necessitate revision of his estimate for the female.

The age at sexual maturity

Earlier estimates of the age of female fin whales at sexual maturity have been discussed in the introduction to this paper (pp. 334–38). These were based on the occurrence of modal groups in analyses of length frequencies, and on methods of age-determination, such as baleen plate, crystalline lens, etc.

Nishiwaki (1957) re-examined this question by comparing the number of laminations in the ear-plug with the number of corpora in the ovaries of 34 antarctic fin whales. He found that 10 laminations corresponded to one corpus albicans and, assuming that laminae are laid down at the rate of two per year, concluded that sexual maturity is attained at 4–5 years. This estimate agrees with his previously published estimate based on other methods (Nishiwaki, 1952). It appears from his fig. 3 that he used six records of immature females (with no corpora) in fitting his regression line, and this would result in a figure for the age at sexual maturity which is slightly low.

Purves and Mountford (1959) correlated sexual maturity with lamination number for a large sample of antarctic fin whales and found that in the female approximately 12 laminations were laid down at sexual maturity. They based this estimate on the youngest pregnant females in their sample, and on their growth curve showing the number of laminae corresponding to the average length at sexual maturity which they assume to be 66 ft. (Actually 65·25 ft. is the best estimate.) They conclude that the age of the female fin whale at sexual maturity is 5–6 years.

Not all females become pregnant at the first ovulation and there is usually a gap of several months between first and second ovulations (see below, p. 416). If all sexually mature females (including those at puberty which have ovulated without becoming pregnant) are examined, a more precise estimate of the age at puberty should be possible.

The ovaries relating to the ear-plugs examined by Purves and Mountford (1959) have now been examined and a brief preliminary account of the findings is helpful at this point. A more detailed account based on a much larger sample of ear-plugs and ovaries now being examined by the author will be published at a later date and may lead to slight modification of the results now put forward. Females are taken to be sexually immature if there is no corpus luteum or corpus albicans in the ovaries; they are sexually mature if the ovaries contain one or more corpora.

Table 13. *Frequency of sexually immature and mature female fin whales in different age groups*

Estimated age (yrs.)	Number		Percentage	
	Immature	Mature	Immature	Mature
1	—	—	—	—
2	1	—	100·0	0·0
3	5	2	71·4	28·6
4	11	3	78·6	21·4
5	7	6	53·8	46·2
6	2	7	22·2	77·8
7	1	7	12·5	87·5
8	—	8	0·0	100·0
9	—	5	0·0	100·0

The results of this study are set out in Table 13 and Text-fig. 34. The estimated ages of individual females are taken from Purves and Mountford (1959, table A) and the material has been confined to area I as their sample from area II is rather small.

In Text-fig. 34 the curve shows the percentage frequency of sexually mature females in different age-groups up to 9 years. The age corresponding to 50% of mature females is about 5 years, which is taken to be the average age at sexual maturity. This is in fairly good agreement with the conclusions of Purves and Mountford (1959); the age above which the majority of females were pregnant was estimated to be about 6 years, but the antarctic catch is taken in January, February and March, and these females would, on average have ovulated during the breeding season (July), that is some 7 months previously, giving an estimate for the age at sexual maturity of about 5·4 years.

Although the average age at maturity is here taken to be 5 years, Text-fig. 34 shows that some 3-year-

old females are sexually mature, while some sexually immature whales are as old as 7 years, a range of 5 years. The full range for the population is probably greater than this small sample indicates.

As regards the male fin whale, Laws and Purves (1956) compared testis weights and ear-plug laminations of a small sample of northern hemisphere animals. They concluded that sexual maturity is attained at 4–6 years. Purves and Mountford (1959) show that the estimated length at sexual maturity (taken to be 63 ft.) corresponds to nine laminations on their growth curve for body length, that is, to $4\frac{1}{2}$ years. Sexual maturity in the male appears, therefore, to be attained at a slightly lower age than in the female.

These estimates of age at sexual maturity are based on an assumed bi-annual rate of lamina formation. Although this appears probable for adult fin whales (see below, p. 467), it is possible that the incremental rate is less regular in immature whales (Chittleborough, 1959, fig. 4), and the laminations are difficult to read. This will probably not greatly affect the estimate of the average age at sexual maturity, but means that the range of ages at which sexual maturity is attained may perhaps be greater.

NEWLY MATURE FEMALES
THE MAMMARY GLAND

Positive identification of newly mature females is made possible in the field by the characteristic appearance (gross and microscopic) of the mammary gland. This is the only group of mature females for which the precise reproductive status is known with certainty. The location of the mammary glands of baleen whales and their anatomy and histology are described by Lillie (1915), Mackintosh and Wheeler (1929), Heyerdahl (1930), Ommanney (1932), van Lennep and van Utrecht (1953) and Chittleborough (1958).

In sexually immature female fin whales the mammary gland is usually not more than 3 cm. deep (mean 2·2 cm.) at the widest part (Text-fig. 35) and is pale pinkish white in colour. It is composed mainly of a mass of connective tissue in which a few small lacteal ducts and blood vessels are seen, and the alveoli are only slightly developed (Mackintosh and Wheeler, 1929, fig. 135).

The glands of females in their first pregnancy (usually with only one corpus luteum and no corpus albicans in the ovaries) are very similar in gross and microscopic appearance to those of immature females and are 3 cm. thick, or less, in the majority (mean 2·9 cm., range 1–6 cm.). The development of the lobules may be slightly greater than in the immature gland, but less than in the resting condition, and the colour remains a pinkish white.

A preliminary study suggested that the mammary gland increases in thickness from the immature level of about 2 cm. to about 4–5 cm. at each ovulation preceding the first pregnancy, and shrinks again to the former level in anoestrus or pregnancy. This would account for the few thicker mammary glands at puberty and the first pregnancy; in spite of their greater depth they retain the immature appearance. Unfortunately the material is insufficient for statistical treatment. There is no evidence for an increase in the thickness of the mammary gland during pregnancy, at least up to the time when the foetus has attained a length of 4·5 m., which is thought to be about a month before parturition (Laws, 1959a). One first-pregnancy female with a foetus 6·4 m. long (which must have been very near term) had mammary glands only 2 cm. thick. Van Lennep and van Utrecht (1953) remark that, 'In contrast to many other mammals the alveoli do not develop until the end of pregnancy'. Chittleborough (1958) found that in humpback whales which were very close to the time of parturition the lobules and alveoli were well developed and colostrum was present in most cases. It is considered unlikely that in fin whales mammary gland development and the secretion of colostrum begin until after they have left the Antarctic on the northward breeding migration.

Lactating females with one corpus albicans in the ovaries will be in their first lactation and in the material there are seven such records. The criterion of full lactation which is adopted here is discussed below (p. 444). During the first lactation the gland undergoes an apparently irreversible change; it may enlarge to over 20 cm. in thickness (mean 16·1 cm., range 8–24 cm.) and although it involutes after weaning (or death) of the calf it does not revert to the former immature condition.

In females which have previously experienced at least one lactation period the mammary glands are either immediately post-lactation in condition or what Mackintosh and Wheeler (1929) termed 'resting' or 'intermediate' between this condition and lactation (see below, p. 444). The mammary glands are then usually more than 3 cm. deep (from 2·5 to 14 cm., Text-fig. 35) and there are brown lobes of coiled ducts set in a thick connective tissue framework (Mackintosh and Wheeler, 1929,
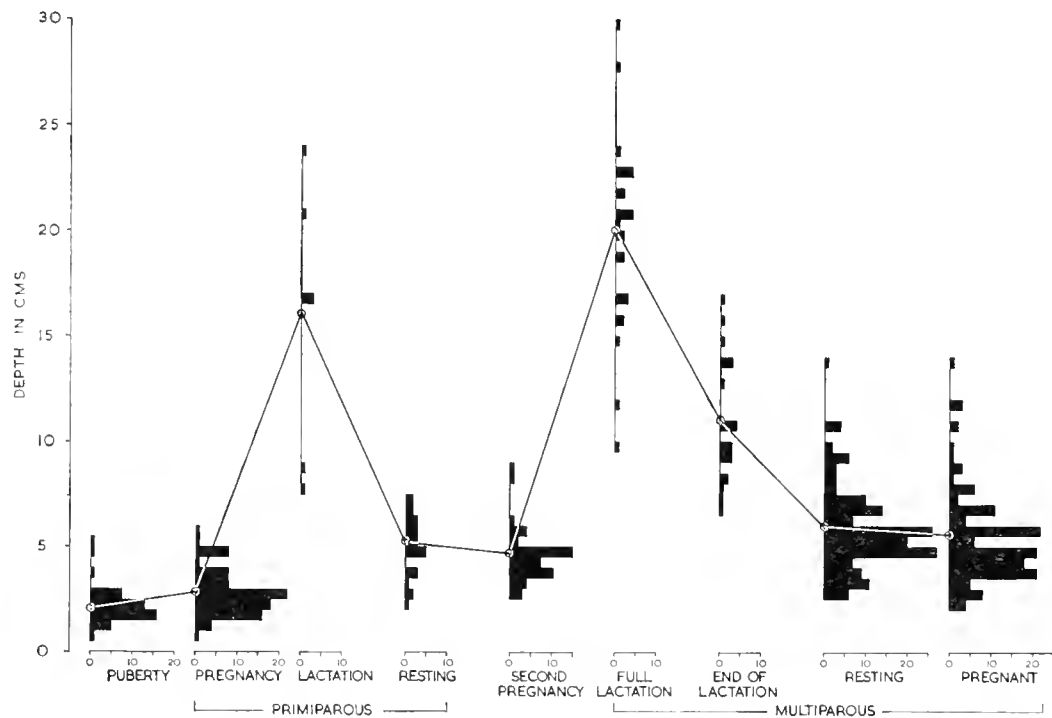
Text-fig. 35. Frequency distribution of mammary gland depth in several groups of female fin whales.

fig. 138; van Lennep and van Utrecht, 1953, fig. 1). Apart from the usually greater thickness, the colour and appearance of 'resting' or 'intermediate' mammary glands is quite different from that of the gland which has not yet been functional. The gross appearance of the mammary gland in section is, therefore, considered to be a reliable criterion of nulliparous or primiparous females.

THE FIRST PREGNANCY

There are 88 pregnant fin whale females in the material which can be classed as primiparous on the grounds outlined above. This figure includes only those individuals for which data on both mammary development and ovaries are available; it excludes females known to be primiparous because they are pregnant with only one corpus luteum and no corpus albicans in the ovaries, but for which no data on the mammary gland condition are available. Of these females, 60 (68 %) had one corpus luteum and no corpus albicans, 20 (23 %) had one corpus luteum and one corpus albicans, 7 (8 %) had one corpus luteum and two corpora albicantia, and one (1 %) had one corpus luteum and three corpora albicantia. They had, therefore, become pregnant for the first time at the first, second, third, or fourth

ovulation and in this class the mean number of ovulations preceding conception was 1·42. Owing to the small size of the sample the variance is quite large. It is of interest that in primiparous females any corpora albicantia will represent unsuccessful ovulations.
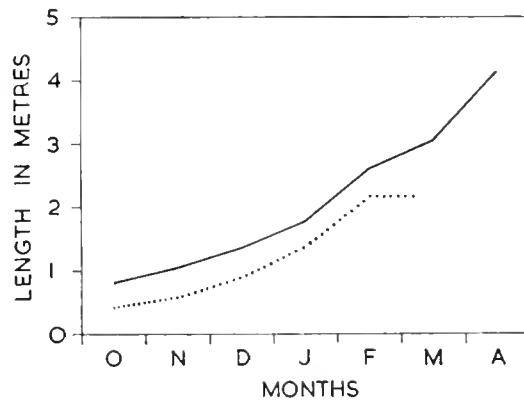
Text-fig. 36. Monthly mean foetal lengths for all pregnant females (solid line) and for primiparous females (dotted line).
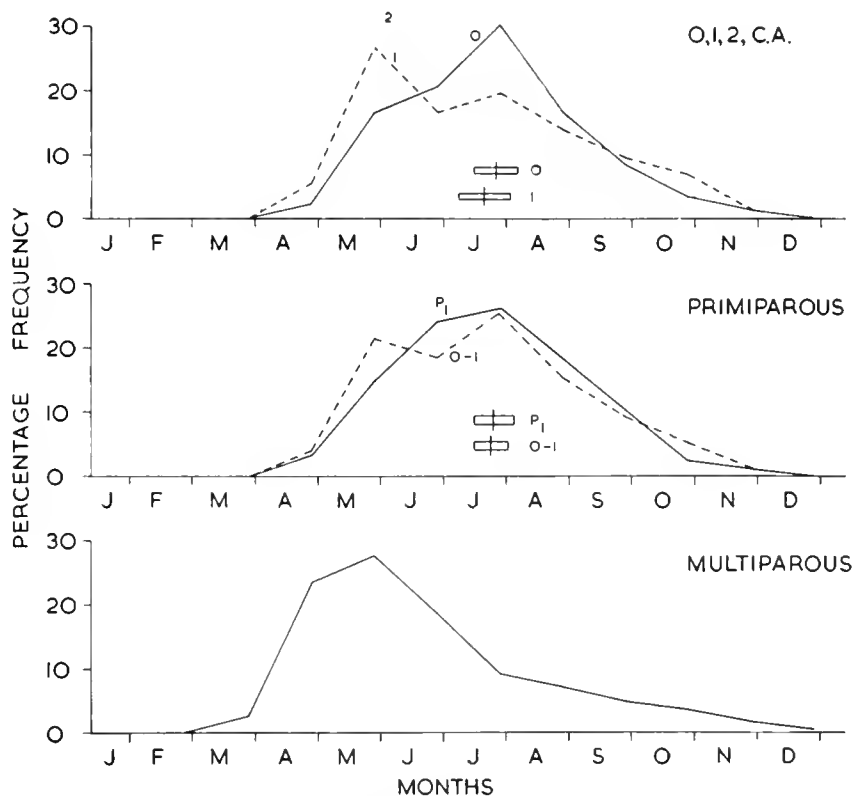
Text-fig. 37. Monthly frequencies of conception for different classes of pregnant females. P_1, first pregnancy diagnosed from mammary glands; o, 1, 2 and o–1, number of corpora albicantia. The mean conception dates ± 2 S.E. are indicated.

There are conspicuous differences in the timing of the pregnancy of primiparous females compared with multiparous females. In Text-fig. 36 the mean monthly foetal lengths for all pregnant females and for females known to be primiparous, from examination of the mammary glands, are set out for comparison. The rates of growth of both groups of foetuses appear to be similar, but the first-pregnancy foetuses seem to be retarded by about a month compared with those of multiparous females.

The monthly frequencies of conception for newly mature females can be estimated by relating the individual foetal lengths to the mean curve of growth as was done previously for all pregnant females (p. 403). This involves the assumption that the rate of foetal growth is the same in primiparous females as in multiparous females; it is thought to be a reasonable premiss and there is no evidence to the contrary. The conception periods estimated in this way for several groups of newly mature females are shown in Text-fig. 37. The classes of newly mature females for which conception dates have been calculated are as follows: (1) Primiparous females with one corpus luteum and up to three corpora albicantia in the ovaries. Examination of the mammary glands is used to diagnose a first pregnancy in this case. They will be referred to as 'primiparous' females. (2) Females known to be primiparous because they are pregnant with a corpus luteum but no corpus albicans in the ovaries, that is, they conceived at the first ovulation. This group includes females for which there is no mammary gland data; it will be referred to as the 'o corpus albicans' group. (3) Females probably in their first or second pregnancy with a corpus luteum and one or two corpora albicantia; to be referred to as the '1 corpus albicans' and '2 corpora albicantia' groups.

The frequency of conceptions of the 'primiparous' group of (88) newly mature females is shown in Text-fig. 37, centre (P_1). The frequency curve is fairly symmetrical, with mean, modal and median dates all approximating to late July (respectively 22, 26 and 21 July). It will be remembered that the conception curve for all females was markedly skewed towards earlier months. The combined conception frequencies of the 'o corpus albicans' and '1 corpus albicans' groups has been plotted in the same figure for comparison with the 'primiparous' group. This is a larger sample (151) and shows a closely similar frequency distribution to the 'primiparous' group, the mean, modal and median dates being very close to these values for the 'primiparous' group (respectively 21, 26 and 19 July). For the purpose of determining the monthly frequency of multiparous conceptions it will, therefore, be assumed that the 'o–1 corpora albicantia' group is equivalent to all first pregnancies (below, p. 425). This means that the samples of primiparous and multiparous females need not be restricted to those females for which mammary gland data are available, but only to those for which the results of examination of the ovaries are available. The number of pregnant females for which foetal length records and ovarian data are available is 845, of which 151, or 17·9 %, are taken to be in the first pregnancy.

Although the frequency curve of 'o–1 corpora albicantia' conceptions is reasonably symmetrical, there is a conspicuous subsidiary peak of conceptions in May and it is instructive to plot the 'o corpus albicans' and '1 corpus albicans' groups separately for comparison. In Text-fig. 37 (top), the conception frequencies of these two groups are plotted and also the conception curve for the '2 corpora albicantia' group. The distribution of the 'o corpus albicans' conception frequencies is very symmetrical with a sharp peak in July (mean and median dates, 23 July; mode 26 July). When the conception curve for the '1 corpus albicans' group is examined, the mean and median dates are found to be at the middle of July (18 July and 12 July, respectively), and the curve is skewed with the mode in May, two months earlier than the peak number of 'o corpus albicans' conceptions. This mode is clearly responsible for the subsidiary peak in the 'o–1 corpora albicantia' conception curve. It will be seen that this advancement of the peak conception date is also characteristic of the '2 corpora albicantia' group, in which it is slightly more marked. When similar curves are plotted for later corpora albicantia groups the proportion of conceptions in April/May is seen to show a marked increase in the '3 corpora albicantia' group and in later groups this becomes the peak month. Wheeler (1930) from his examination of the frequency of numbers of corpora concluded that in the first sexual season the majority of females become pregnant at the first ovulation, while in subsequent seasons unsuccessful ovulations usually precede pregnancy. In explanation he suggested that whales nearing puberty tend to stay near the breeding areas, or at any rate do not make a long southward migration, so that they

are first to be impregnated, while older females arrive on the breeding grounds later, after one or more unsuccessful ovulations. In fact it is now known that the pubertal females migrate and conceive later than the mature females. The tendency for the advancement of the pairing season with increasing age is further discussed below (p. 427).

Growth in length just after puberty

Females in the 'o corpus albicans' group form a distinct, narrow, and relatively uniform class of animals. For this group of females it is possible to study the rate of growth over almost a year by comparing the maternal growth with the growth of the foetus. The average curve of foetal growth in length of the fin whale has been established with reasonable accuracy (p. 403), and may be used as an absolute time-scale over the period of gestation.
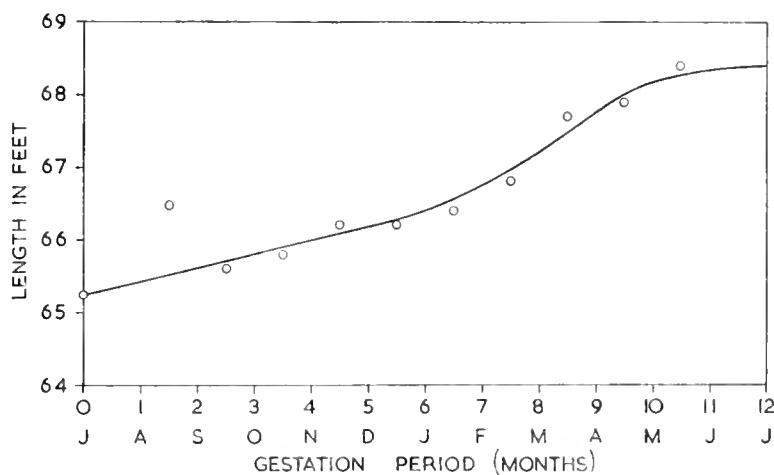
Text-fig. 38. Probable growth in length during first pregnancy of females which conceived at the first ovulation.

The mean length at conception is taken to be 65·25 ft. (see above, p. 406), but this may be a slightly high (or low) value because females which become pregnant at the first ovulation may be shorter (or longer) than those which ovulate unsuccessfully for the first time.

The mean lengths of 86 primiparous females in the 'o corpus albicans' group are set out in Table 14, according to the month of pregnancy, and in Text-fig. 38 the smoothed maternal lengths are plotted against the months of pregnancy, taking July as the mean period of conception. A growth curve has been fitted by inspection to these points taking its origin at a length of 65·25 ft. at conception. There is no statistical justification for fitting an approximately sigmoid curve to the points, but with the exception of the second point, which represents a small sample, the lightly smoothed mean lengths do not show large fluctuations and it is reasonable to suppose that the average curve which has been drawn does approximate to the true growth curve (Text-fig. 38). It is significant that the supposed maternal increase in growth-rate begins about 6–7 months after conception; it is at this time that the exponential phase of foetal growth begins (p. 401, Text-fig. 30) and this increased growth is related to the short annual period of intensive feeding. A mass curve of this kind is likely to reduce apparent changes in the growth rate. It is likely, therefore, though not proven, that fin whales experience a period of increased growth in length, similar to the increase in weight known to take place on the antarctic feeding grounds (Ash, 1956). Probably all fin whales show a similar rapid seasonal increase in length on the feeding grounds, which yearly becomes smaller and smaller until physical maturity is attained. These data suggest that just after puberty the average rate of growth is between 2 and 4 ft. a year, probably just over 3 ft.

Table 14. *Growth of the '0 corpus albicans' group of females during the first pregnancy*

Duration of pregnancy (months)	Sample size	Length (ft.)		
		Range	Mean	Smoothed (threes)
0–1	2	(63·0–67·5)	65·3	—
1–2	2	(69·0–71·0)	70·0	66·5
2–3	1	—	62·0	65·6
3–4	7	(63·0–66·0)	64·9	65·8
4–5	6	(62·5–70·0)	67·4	66·2
5–6	16	(62·0–70·0)	66·3	66·2
6–7	15	(60·0–78·0)	66·3	66·4
7–8	5	(64·0–71·0)	66·8	66·8
8–9	20	(63·0–72·0)	67·7	67·7
9–10	8	(67·0–70·0)	68·3	67·9
10–11	3	(61·0–72·0)	67·7	68·4
c. 11	1	—	71·0	—

Table 15. *Mean length and variation in six groups of newly mature females*

	Number	Mean length	σ	2 S.E.
A Puberty	166	65·25*	2·07	0·32
1 Ovulation				
B Primiparous	90	66·9	2·66	0·58
C Nulliparous	31	66·8	2·90	1·04
B + C	121	66·9	2·73	0·50
D Lactating or Resting	31	68·5	2·40	0·86
2 Ovulations				
E Nulliparous and Primiparous	32	68·2	2·81	0·99
F Second pregnancy	21	68·9	2·36	1·03

* This is the intersection of the length frequency distributions of immature and mature females; the standard deviation and standard error are calculated from the frequency distribution of the overlapping group (see Text-fig. 33).

Further information about the average rate of growth in length in the period following puberty can be obtained by considering the average lengths of these and other groups of females known to be recently mature. The means plus or minus one standard deviation and two standard errors are given for each of five groups of recently mature females in Table 15 and plotted in Text-fig. 39. The groups comprise (*a*) females at puberty; females which have ovulated once and are (*b*) primiparous, (*c*) nulliparous, or (*d*) lactating or resting; females which have ovulated twice and are (*e*) nulliparous or primiparous, (*f*) in the second pregnancy. (In the groups (*d*) and (*e*) the two categories comprising the group have been amalgamated so as to increase the size of the sample for statistical treatment.) With the exception of the nulliparous females, these all represent individuals which became pregnant at the first ovulation and are presumed on average to have attained puberty in July (that is, as primiparous '0 corpus albicans' females). The average date of the other observations is mid-February. The probable mean growth curve of first pregnancy, '0 corpus albicans' females (from Text-fig. 38) has been drawn in as an unbroken line. It passes close to the mean length of the primiparous '0 corpus albicans' group (B) and through the mean of the nulliparous '1 corpus albicans' group (C). Females in their first lactation, or first resting period with one corpus albicans (D) will be on average a year older than the primiparous '0 corpus albicans' group, and have been plotted in the second year following puberty. It is possible that a *very small* proportion of the resting females in this group may be older.

The mean growth curve has been continued as a broken line, increasing very slightly from June to December and then increasing again during the second feeding season after puberty. At 2 years after puberty the mean length is shown as 69·6 ft. If the average rate of ovulation is 1·4 per year (below p. 465) then 2 years after puberty there are expected to be on average 2·8 corpora and from Text-fig. 25 the mean length at 2·8 corpora is 69·6 ft. The growth previous to puberty is also suggested as a broken line, to indicate that in the feeding season before puberty growth is more rapid, as is probable in the primiparous feeding females. If this line of argument is correct, then puberty usually succeeds both a period of rapid growth, and a northward migration when day length is increasing (see below, p. 421).
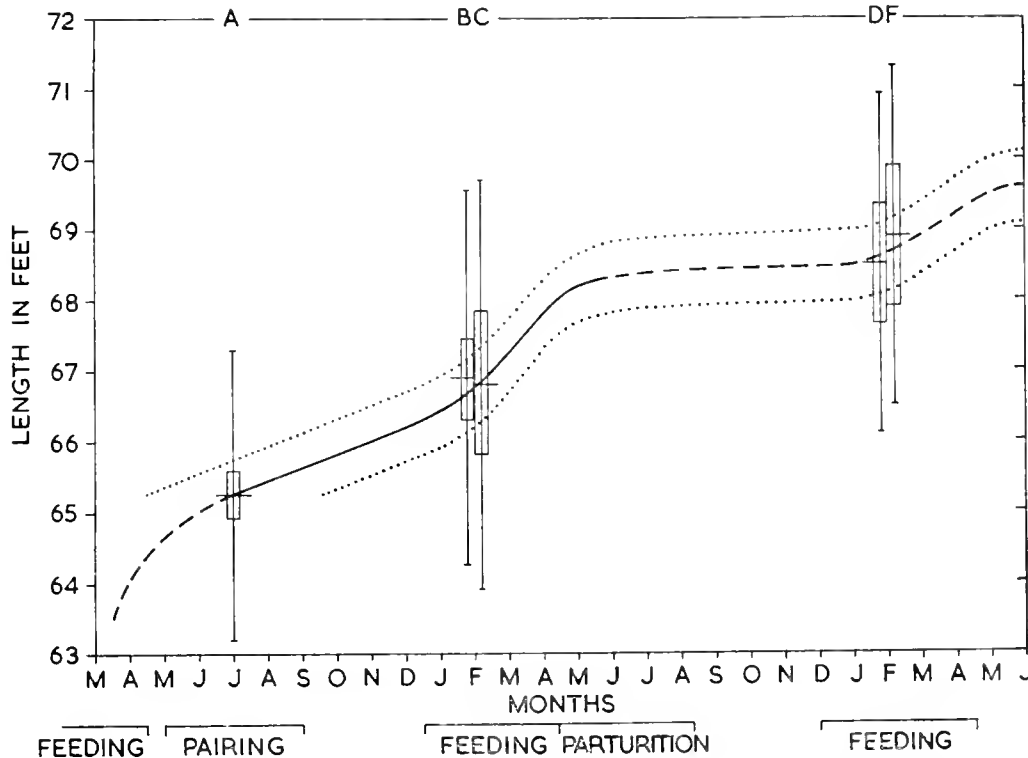
Text-fig. 39. Growth of newly mature females indicated by mean length ± σ, ± 2 s.e. A, at puberty; B, first pregnancy, o corpus albicans; C, one nulliparous ovulation; D, first lactation or resting period; F, second pregnancy, 1 corpus albicans. See text for explanation.

The position of the remaining group, of females in their second pregnancy with one corpus albicans and resting mammary glands (F), must now be discussed. These are females which have become pregnant again at the first ovulation after the termination of the first pregnancy. It seems most probable that the origin of this second pregnancy is either a post-partum ovulation (shown below, p. 429, to be a normal feature of the reproductive cycle in female fin whales and some other species) and/or an ovulation following the termination of lactation upon loss of the calf. It is, however, certain that some, possibly all, of these first-lactation females do not experience a post-partum ovulatory period and that some or all of them are a year older than has been indicated in Text-fig. 39. It is only possible to diagnose accurately the reproductive history of those females in the first lactation or resting period which have only one corpus albicans in the ovaries. None of the individuals in this group has, by definition, experienced a post-partum ovulation. Those with more than one corpus in the ovaries might possibly be in the second lactation or resting period, but there are undoubtedly many females in their first lactation or resting period which have more than one corpus albicans in their ovaries and some of these may well have experienced a post-partum ovulatory period. The fact

that the mean of this second-pregnancy group is so close to the mean length of females in their first lactation or resting period, suggests that the original assumption is correct and that this group is correctly placed in Text-fig. 39.

The variance in length in each group is rather large (standard deviations 2–3 ft.). The dotted lines in Text-fig. 39 represent the mean plus or minus 6 in. and this represents the probable range of error in the mean curve taking into account the values of two standard errors of the mean lengths at puberty, some months later (groups (b) and (c) combined), and over a year later (groups (d) and (e) combined).

THE FIRST OVULATIONS

We have seen that prior to the first pregnancy there may be from one to four ovulations, with a mean number of about 1·42. There are two important questions which we must now attempt to answer. First, is ovulation spontaneous or is it induced by the stimulus of coition? Secondly, what is the length of the oestrous cycle and the interval between successive ovulations; that is to say is the fin whale polyoestrous or monoestrous?

Ovulation is probably spontaneous as in ungulates and most other mammals (Eckstein, 1949). Mackintosh and Wheeler (1929, p. 381) describe the vaginal band which is present in about 21% of immature females. This structure is so placed that it is almost certain to be ruptured when mating occurs and up to 1957 no intact vaginal bands had been observed in parous females. Wheeler (1930, p. 413) mentions the case of a female fin whale with immature mammary glands, an unbroken vaginal band and one corpus albicans in the ovaries; a similar case was recorded by Mackintosh and Wheeler (1929, p. 390), and there have been a few later unpublished records of females in a similar condition. This is a rarely observed condition because, of a hundred females at puberty, about 70 become pregnant at the first ovulation, and only about 21% of the remainder would have a vaginal band; this means that less than about 6% of females which have ovulated only once can be expected to have an unbroken vaginal band. The presence of corpora in the ovaries of females with unbroken vaginal bands would appear to be conclusive evidence of spontaneous ovulation. However, in 1958 D. F. S. Raitt, a biologist making observations and collections for the National Institute of Oceanography, reported a pregnant fin whale which had an unbroken vaginal band. 'One case appeared to be an example of a virgin ovulation. This was a 69 ft. fin.... The vaginal band was intact, though rather slack, the mammary gland was 4·5 cm. deep and a 10 ft. 11 ins. male foetus was found. The ovaries were obtained and one had an apparently functional corpus luteum (unpublished report). In spite of this one exceptional record it is considered that the several other cases of virgin ovulations associated with unbroken vaginal bands are evidence that ovulation is spontaneous. Some additional support for this assumption is provided by the relatively high proportion of non-pregnant females in antarctic waters which have recently ovulated (pp. 418 and 436), although mating behaviour has been very rarely observed.

It has been shown that some 68% of newly mature female fin whales become pregnant at the first ovulation. Furthermore, a large proportion of newly mature females, taken in the Antarctic several months after the pairing season, have ovulated only once and regression of the corpus albicans representing that ovulation is already advanced (mean diameter 4·4 cm.), indicating that it represents a monoestrous cycle, and not the first of a series of polyoestrous cycles. The great majority of fin whale females, if not all, are, therefore, effectively monoestrous in their first sexual season. Some 32% of females in their first pregnancy had ovulated more than once before becoming pregnant. It is not possible to say how long the oestrous cycle in the fin whale is, but it is probably about 16–23 days as in ungulates (Eckstein, 1949) or longer; it is very unlikely to be shorter than this. Then, if the female fin whale is polyoestrous in the first sexual season the curves of the monthly frequency of

conceptions for the 'o corpus albicans' group and the 'primiparous' animals with o–3 corpora albicantia (diagnosed from mammary gland inspection) should differ. The latter group might be expected to show more conceptions in the later months. In fact a comparison of these curves (Text-fig. 37) shows that they are almost identical.

Curves showing the frequency of conception in those females which had ovulated twice or more before the current pregnancy have already been presented (Text-fig. 37). The '1 corpus albicans' group was shown to be in advance of the 'o corpus albicans' group in this respect, whereas, if fin whale females are polyoestrous it would be expected to be slightly later. The '2 corpora albicantia' group shows a similar advancement.

The majority of the '1 corpus albicans' group will probably be primiparous, but some of this group may be individuals which are in the second pregnancy, having failed to complete the first pregnancy. In this event the second ovulation, leading to the current pregnancy, would probably have occurred earlier in the pairing season than the first ovulation ('o corpus albicans' group) as is the tendency in multiparous females.

Others may be females which became pregnant a second time as a result of a post-partum ovulation (see p. 429) following the successful completion of the first pregnancy. If pregnancy were to last 11¼ months in primiparous females, as in multiparous females, and this ovulation is about 3–4 weeks post-partum then the group would tend to conceive about the end of July. This would partly counter the effect of earlier mating of females in which the first pregnancy had been prematurely terminated.

The evidence presented above, although not conclusive, suggests that at puberty there is a single ovulation and that if pregnancy does not intervene the female usually goes into anoestrus without further ovulatory cycles. It is possible that a small proportion of females do experience up to three or four polyoestrous cycles, but this is thought to be unlikely.

Chittleborough (1955b, p. 318) implies that this is also true of the humpback whale. He states that some female humpback whales become pregnant at the first ovulation, but that the ovaries of a number of nulliparous females 'contained one (or sometimes two) corpora albicantia' and these females 'would probably have become pregnant for the first time during their second ovulatory season'. Presumably regression of the corpora albicantia was well advanced in these females and the follicles were not undergoing pro-oestrus enlargement. The mean length of these females was about a foot more than the mean length at puberty which also suggests, as in the fin whale (Text-fig. 39C), that puberty occurred some months earlier.

Certain evidence, now to be presented, shows that puberty may be attained outside the usual pairing season, and that in this case also the cycle at puberty is monoestrous.

In the material there are 10 virgin females which have a corpus luteum of ovulation in the ovaries. In seven of these animals (taken between November and February) this was the result of the first ovulation at puberty; in one (20 January) it represented the second ovulation, and in two others (11 November, 18 January) it was a product of the third ovulation. These are diagnosed as virgin ovulations from the virgin appearance of the mammary gland, and the absence of any embryo in the uterus. Only 2·4% of all pregnancies are estimated to begin in the 4 months November–February (Table 11).

In one of these females (taken on 29 December) regression had begun but the corpus was still 7 cm. in diameter. The others were taken between 15 November and 14 February, and the corpora lutea ranged in size from 6 to 13 cm. The mean diameter was 8·8 cm., which is slightly higher than the mean diameter of the corpus luteum of ovulation, but well within the probable range of variation of the mean (8·28±0·82 cm., above, p. 356). It is well below the mean diameter of the corpus luteum of pregnancy (11·44±0·15 cm.). This supports the diagnoses of recent ovulations. In the three nulliparous

females which had ovulated more than once the diameters of the largest corpora albicantia were 4·5, 3·3 and 3 cm. respectively, suggesting that there had been quite a long interval between the last two ovulations and that they do not represent successive ovulations in a polyoestrous ovulatory cycle.

The estimated pairing season for the 'o corpus albicans' group is April–November (inclusive) (Text-fig. 37). The present material shows that puberty can be attained and the first ovulation take place several months before or after the normal pairing season for this group. March is the only month for which there is no record or estimate of a female fin whale reaching puberty.

For six of these females observations on the extent of the diatom film were made. In three of them there was no diatom infection (two in January, one in February); in one (November) it was incipient; in one moderate (November); and in one it was heavy (December). The latter record relates to the female in which the recent corpus luteum had just begun to regress. As the diatom film is acquired in antarctic waters these limited data suggest that the corpora lutea of ovulation in these whales formed during or just after the southern migration.
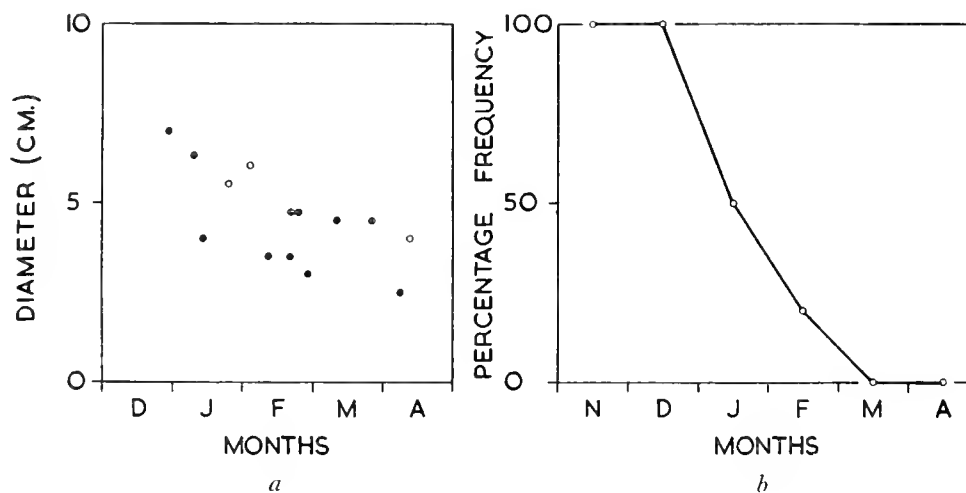
Text-fig. 40. *a*, Size of largest corpus albicans of 14 nulliparous females without a corpus luteum; antarctic material. (Black circles, only corpus albicans; white circles, largest of two or more corpora albicantia.) *b*, Monthly frequency of ovulation of 41 pubertal females taken in the Antarctic.

Certain other evidence supports this hypothesis. There are records of the size of the largest corpus albicans in a number of pubertal nulliparous females taken in the Antarctic. In Text-fig. 40, *a*, the diameters of 14 such corpora (from ovaries in which there are no active corpora lutea) are plotted according to the date of collection. They show an apparent decline in size, probably representing the shrinkage associated with regression. The sizes of these corpora suggest that most of them were derived from corpora lutea of ovulation which formed as late as November, December, or January. The ovaries of these females do not contain follicles undergoing pro-oestrus-enlargement and this confirms that these corpora do not represent the first ovulation in a series of dioestrous cycles.

If we now examine the entire group of pubertal nulliparous females (which incorporates animals not included in the discussion above because there were no records of corpora size for them) we can obtain a better estimate of the time of ovulation. This material comes from each of the 6 months November–April and for each month the percentage of animals in this group which have an apparently active corpus luteum of ovulation in the ovaries (as opposed to those in which the ovaries contain one or more corpora albicantia) has been calculated. This is shown in Table 16 and graphically in Text-fig. 40, *b*. A single record for 29 December is the animal mentioned above in which the corpus luteum had only just begun to regress and had characteristics of both corpus luteum and corpus albicans.

This has been placed in December as a corpus luteum of ovulation and in January as a corpus albicans.

The paucity of records in the early months does not permit a precise estimate of the peak time of ovulation during this period, and the purpose is merely to show that there is an ovulatory period in this group of pubertal females which is well outside the main breeding period (see also pp. 403–6). From the evidence presented in Text-fig. 40, it is presumed that before January the majority of pubertal females present in the Antarctic have recently ovulated, and that after January the ovaries of the majority contain young regressing corpora albicantia from recent ovulations. This evidence also suggests that an ovulatory period is associated with the southern migration which probably takes place in the majority of this group in November, December, and January, but may be slightly earlier or later.

Table 16. *Monthly frequency of ovulation of pubertal female fin whales taken in the antarctic*

	Total ovulated nulliparous females	Corpus luteum of ovulation		Corpus albicans	
		No.	Percentage	No.	Percentage
November	2	2	100	0	0
December	1*	1*	100	0	0
January	11	6	50	5(+1*)	50
February	10	2	20	8	80
March	11	0	0	11	100
April	6	0	0	6	100
Total	41	11	—	30(+1*)	—

* This record has been included as corpus luteum and corpus albicans; see text p. 418.

One anomalous pubertal female has not been included in Text-fig. 40, *a*, for reasons given below, but is included in Text-fig. 40, *b*. This individual was taken on 24 January and had one corpus aberrans in each ovary (see p. 380), measuring 2·5 and 2·3 cm. in diameter. The largest follicle was 3·5 cm. in diameter and there were several follicles about 3 cm. in size, in each ovary. This female had not yet acquired a diatom film and is, therefore, presumed to have recently completed a southern migration during which ovulations took place which led to the formation of corpora aberrantia. It does not invalidate the conclusions put forward above.

The monthly variation in size of the largest follicle in the ovaries of females approaching puberty (over 63 ft. in length) has been discussed above (p. 346, Table 2, Text-fig. 3). In conjunction with the foregoing evidence it is significant that the largest follicles are found in females of this group taken in the Antarctic in November. The mean size of the largest follicle in three individuals taken in November is 3·3 cm., and the absolute maximum size of follicles in immature females was about 5 cm. for one of these November animals. From January to May the monthly mean maximal follicle size is about 1 cm. or less. The large size of the November follicles suggests pro-oestrus enlargement which might or might not have been followed by maturation and ovulation.

For the present it is sufficient to show that ovulations can occur outside the recognized pairing season, and that then also there is a single ovulation, almost invariably unsuccessful probably because the majority of males are not then in breeding condition. There is no evidence for a succession of several ovulations at intervals of a month or less. The evidence presented below (p. 438) suggests that this is also true of multiparous females which ovulate outside the usual breeding season.

One other separate piece of evidence which is inconclusive when considered alone, but which appears to fit this hypothesis better than any other, remains to be discussed. In Text-fig. 41 the mean length, plus or minus one standard deviation and two standard errors, is set out for two groups of newly

mature females which have ovulated only once (A) or twice (B). These data are presented in Table 15, groups B + C and group E respectively. The probable range of error of the estimated mean growth curve for females which attain puberty in the breeding season at a mean length of 65·25 ft. (from Text-fig. 39) is also shown by the dotted lines. The mean date of sampling is mid-February.

When the mean length of the once-ovulated group is compared with that of the twice-ovulated group there is seen to be a difference of 1·3 ft. The standard error of the difference between these two means is 0·554, which means that the difference is statistically significant. If the twice-ovulated group
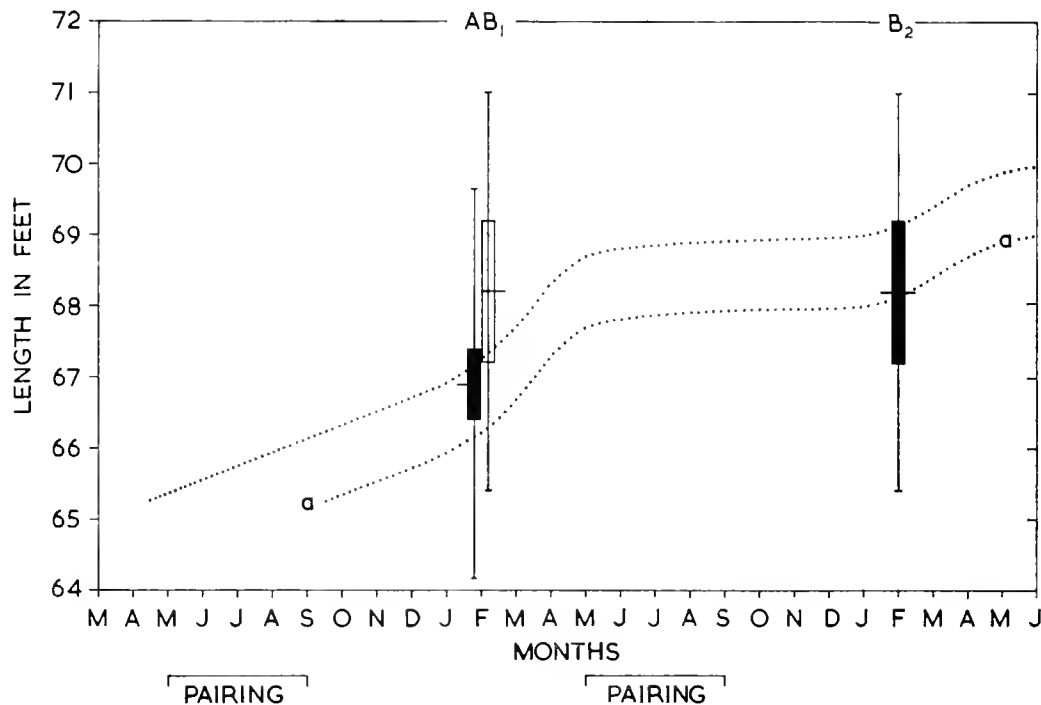
Text-fig. 41. Growth of newly mature females. The mean lengths $\pm \sigma$ and 2 s.e. of nulliparous or primiparous females which had ovulated twice (B_1, B_2) are duplicated one year apart for comparison with the growth curve of once-ovulated, nulliparous or primiparous females (A). See text for explanation.

attained puberty and ovulated at about the same time as the once-ovulated group it is very unlikely that there would be such a discrepancy between the mean lengths of the two samples. The mean values for the once-ovulated females which were primiparous or nulliparous (Text-fig. 39 B and C) are in very close agreement with each other.

If the twice-ovulated group is plotted a year later (B_2) its mean length (68·2 ft.) is seen to be close to the length (68·5 ft.) of the group of females known to be in their first lactation or resting period (Table 15). That is to say, pregnant females in the '1 corpus albicans' group probably become pregnant about a year later than the '0 corpus albicans' group. The mean length of the twice-ovulated group under consideration coincides with the estimated lower limit of the growth curve of the '0 corpus albicans' group of pregnant females (Text-fig. 41, curve a···a) which on average attain puberty and pair in July. The estimated time of pairing of the '1 corpus albicans' group is also July (Text-fig. 37), when this lower curve (a···a) has attained a length of nearly 68 ft., which is nearly 3 ft. more than the mean length at puberty. It will be remembered that the growth in length in the first year after puberty was taken to be just over 3 ft. The origin of this curve (a···a) at the mean length at puberty is in October, some months after the peak pairing season, but having regard to the length variance of the group concerned they could well have attained puberty as late as December or January.

The question is now, when the first ovulation of the ' 1 corpus albicans' group of pregnant females occurred. This could have been at the time when the average length and age at puberty was reached, or possibly at an average length of about 68 ft. just before the second ovulation which led to the current pregnancy. It seems most probable, taking into account all the evidence discussed in the preceding pages, that the pregnant ' 1 corpus albicans' group is composed of females which attain puberty at a later date than the pregnant 'o corpus albicans' group, during or just after the southward migration, say in December or January. Pubertal females which were taken in the period November–February and are discussed above (p. 417) belong to this group. After one ovulation they probably go into anoestrus and conceive on average in July at the next ovulation after the northward migration to the breeding grounds.

PUBERTY AND ITS RELATION TO THE MIGRATORY CYCLE

It has been shown that the gross structure of the mammary gland is diagnostic of nulliparous or primiparous female fin whales. This enables certain groups of pubertal or newly mature females to be defined and distinguished, and simplifies investigation of events at this stage of the life-cycle. It is estimated that, on average, puberty is attained at an age of about 5 years (range 3–8 years), corresponding to an average length of 65·25 ft. The standard deviation of the mean length at puberty is 2·07 ft. which means that 95% of females should attain puberty between about 61 and 69 ft., and 67% between 63 and 67 ft. Asdell (1946, p. 10) states that of the factors associated with puberty length is much less variable than age, and this is true of the fin whale also. Laws (1956b) has shown that there is a very close relation between growth and sexual maturity in whales as in other mammals. For 10 species of cetaceans the mean length at puberty expressed as a percentage of the mean length of physically mature animals averages 85·1% ($\sigma = 3\cdot14$, $V = 3\cdot69$). It should be mentioned that the true length variance at puberty (and in other age-groups) in the fin whale is probably rather less than that given. Errors in length measurement are undoubtedly relatively large; the dragging of a 60-ton whale up the slipway against gravity and friction might be expected to extend the whale by an amount which should vary according to the post-mortem history. The true mean length at puberty is, therefore, even less variable than the figures given above suggest. The average rate of growth at puberty is about 3 ft. a year, and in the majority of females puberty is preceded by a period of intensive feeding in the Antarctic, when growth is probably rapid and follicular development may be stimulated by the improved nutritive state. Maximum fertility is probably not reached until after the attainment of physical maturity (p. 456).

Ovulation is almost certainly spontaneous, and about 70% of females become pregnant at the first ovulation. The curve of monthly frequencies of conceptions is very symmetrical for this group, and the pairing season, which apparently extends from April to October or November, is later in the year than the pairing period of multiparous females.

A number of nulliparous females are found in the Antarctic between December and April which have only one corpus albicans in the ovaries. Thus a single ovulation appears to be the rule in the first ovulatory period even in the absence of conception. Furthermore, it is found that in general females which become primiparous at the second ovulation conceive earlier in the year than those females which become primiparous at the first ovulation. This also suggests a monoestrous cycle at puberty, for if there were two or three cycles in succession females which conceive at the second or third ovulation should in general pair rather later than females which become pregnant at the first ovulation.

The evidence strongly suggests that there is a second, subsidiary, period when females which did not attain puberty in the pairing season (April–November) ovulate during or just after the migration to the antarctic feeding grounds. Pubertal females are found in antarctic waters which have recently

ovulated, with a corpus luteum of ovulation in the ovaries, and have not yet acquired a diatom film. The most recently formed corpora albicantia in the ovaries of other nulliparous females taken in antarctic waters appear to have been derived from corpora lutea formed as late as November, December, or January, and this is associated with a decline in the percentage of pubertal females with corpora lutea of ovulation in the ovaries from January onwards. This subsidiary ovulatory period also represents a monoestrous cycle and rarely, if ever, initiates a pregnancy. A period of anoestrus succeeds, and the next ovulation, which probably follows a northward migration, occurs in April–November when this group of females have probably attained on average a length of about 68 ft. This ovulation is usually succeeded by pregnancy.

The type of sexual cycle described in this short summary is very different from the type of cycle which has previously been assumed to apply to cetacea. Hitherto it has been assumed that whales have a series of polyoestrous cycles during a single protracted ovulatory period. It has been assumed that an individual female may experience several dioestrous cycles at intervals until interrupted by pregnancy or anoestrus. The new evidence about the fin whale suggests that this species is not usually polyoestrous but rather that it is seasonally monoestrous, and further evidence is presented in a later part of this paper (p. 425) which shows that the annual cycle of multiparous female fin whales is also characterized by two ovulatory periods, which probably represent two monoestrous cycles.

If the arguments put forward above are valid then there are two seasons of the year at which fin whale females may attain puberty. The majority, probably about 70%, ovulate for the first time in winter during the usual pairing season (April–November) after a northward migration, and the others probably attain puberty and ovulate for the first time in spring and summer (September?) (October–February), after a southward migration. This is a very unexpected conclusion and it is worth looking into possible exteroceptive factors which may be responsible.

A majority of mammals (insectivores, rodents, non-ruminant ungulates and carnivores) are spring breeders and, as Marshall (1922) pointed out, they appear to be sensitive to increasing light. A minority (the ruminant ungulates) are autumn and winter breeders and would appear to be sensitive to decreasing amounts of light; others appear to be uninfluenced by seasonal changes in the amount of light. Other factors such as temperature, humidity, food, etc. are also important.

'The various factors which affect the time of the appearance of puberty probably act through the pituitary-gonad mechanism. Such exteroceptive factors, too...as the length of daylight changes during the course of the year which cause the onset of the breeding season will accelerate or retard the age of puberty according as the normal age for puberty in the individual falls before or after this season' (Hammond and Marshall, 1952, p. 824). Thus for certain breeds of sheep the breeding season extends from September to March and those lambs born early in the season will be longer in arriving at the age of puberty than those born later in the season. In sheep there is neither a fixed age at puberty nor a fixed time of year for the first heat (J. Hammond, Jr., 1944). Sexual activity begins at a minimal age of about 6 months, and with increasing age the threshold of stimulation required to produce the first oestrous cycle falls, until by about 10 months it reaches the adult level. The sheep responds to decreasing light, and as day length decreases so the intensity of stimulation increases. It is maximal at the middle of the breeding season which corresponds to the minimal age at first heat (about 6 months). If this age is reached later in the breeding season the intensity of stimulation is not sufficient to bring about oestrus, and puberty is not attained until the next breeding season when the animal may be over a year old (Hammond and Marshall, 1952, p. 824).

A similar mechanism appears to be operative in the case of the fin whale except that this species probably responds to increasing light, attains puberty at a much greater age and, owing to the migratory habits, experiences two periods of increasing day length each year instead of one (see below).

In most terrestrial mammals the migratory movements, if any, are restricted by geographical or physical barriers. The scale of migration is greatest in those animals, such as fish, birds, bats, seals and whales, which live in a continuous medium and are less restricted in their movements by such barriers. Whales appear to undertake longer migrations than other aquatic mammals. Some seals migrate over a latitude range of about 25°: the migratory range of the northern fur seal (*Callorhinus ursinus*) is from about 35° N. to about 60° N. (Kenyon and Wilke, 1953), and the harp seal (*Phoca groenlandica*) travels between 45° N. and about 70° N. (Nansen, 1925), although some individuals may cover a greater distance. On the other hand, the humpback whale regularly migrates between the breeding area in about 15° S. latitude and the antarctic feeding zone at about 66° S. (Dawbin, 1956, p. 193). The grey whale (*Eschrichtius glaucus*) migrates between a feeding area in the North Pacific at about 60° N. and a very restricted breeding area centred on lower California in latitude 25° N. (Gilmore, 1955). The fin whale undertakes similar annual migrations, though the evidence is
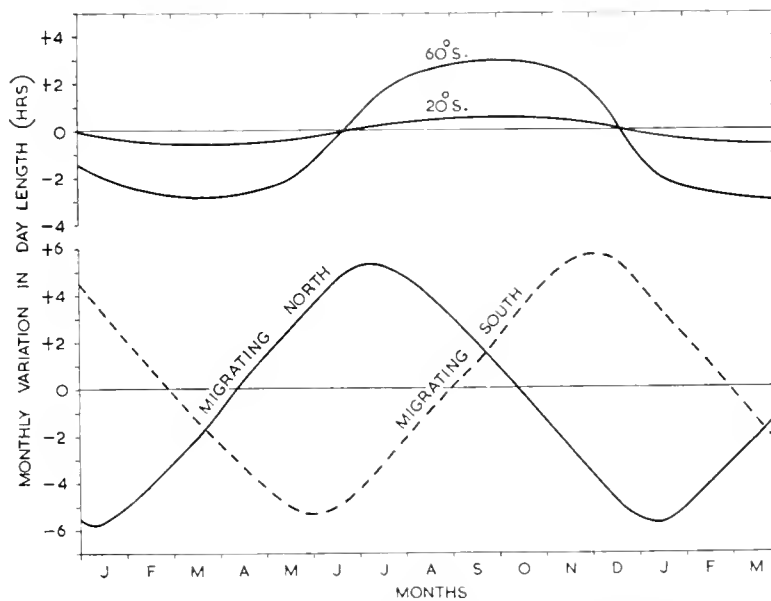
Text-fig. 42. Above, monthly changes in day length (sunrise to sunset) at latitudes 20° S. and 60° S. Below, estimated monthly changes in day length experienced by whales migrating between 20° S. and 60° S.

not so complete (see above, p. 339), and in its breeding range the fin whale is probably more widely dispersed than the humpback. One result of these migrations is that the fin whale, and other whales, are subjected each year to two periods of increasing daylight hours and two periods when day lengths are decreasing. Animals which do not migrate experience only one period of increase, and one of decrease, in day lengths.

Let us assume for present purposes that the fin whale migrates between a breeding area, centred on about 20° S. latitude, and a feeding area which is for the most part south of 60° S. Let us also assume that the migration between these latitudes takes about a month. The change in the length of day which would be experienced by animals migrating north or south in each month is shown in Text-fig. 42. From this it is evident that animals migrating north in April, May, June, July, August and September should experience increasing lengths of day with the maximum rate of increase influencing animals migrating between the beginning and end of July and amounting to some 5 hr. Animals migrating southwards in September, October, November, December, January and February should also experience increasing daylight hours with a maximum rate of increase in November and December. It can be shown that two cycles of increasing photo-periods would also be experienced if we assume alternative latitudinal movements, such as between 15° S. and 65° S., 30° S. and 60° S., 40° S. and

60° S., and so on. If it is assumed that each migration takes longer than a month, then the changes in day length also show two periods of increasing photo-period. Animals remaining at any one latitude in the southern hemisphere are subject to increasing lengths of day from July to December, though the rates of increase are in general much smaller than those experienced on migration.

We may now turn to the question of when females approaching the age of puberty make their northern migration. Mackintosh (1942) discussed the monthly frequency of immature females on the feeding grounds. He shows that both at South Georgia and on the pelagic whaling grounds the average length of the catches falls, and the proportion of immature females in the catches (calculated from the mean length of puberty) increases in the later part of the summer season. Although this change in the composition of the catches is more marked in blue whales than in fin whales, it suggests that immature female fin whales arrive at and probably depart from the antarctic feeding grounds later than the adult females. A similar conclusion was reached by Hjort, Lie and Ruud (1935) and by Ottestad (1938).

Mackintosh and Brown (1956, fig. 2, table 1) show that the population of large baleen whales (blue, fin and humpback) in antarctic waters is at its peak in February, but there are still large numbers present in March and April. Thus, expressed as whales observed per hundred miles steamed, there were 9·9 in February, 7·2 in March and 3·6 in April. Allowing for the area of ice-free water in three surface temperature zones the calculated population in April is rather more than half that present in February. The sampling in May and June, when the estimated population south of the Antarctic Convergence is higher, is considered by the authors to be unsatisfactory and unrepresentative of the Antarctic as a whole. Nevertheless an appreciable number of whales are probably still present in these months and the great majority of these are likely to be fin whales both because fin whale populations are larger than the stocks of the other species and because the feeding season for blue and humpback whales is in advance of the season for fin whales (Mackintosh, 1942).

If we are correct in assuming that a large proportion of this rearguard are immature females, then the main northward migration of fin whale females approaching maturity probably takes place from April onwards. They will be subjected to maximal stimulus from increasing day length on migration during July (Text-fig. 42). This is the peak month of pairing for those females which become pregnant at the first ovulation (Text-fig. 37). Animals migrating northwards in May and June and in August and September will also be subject to increasing day lengths although the rate of increase will be smaller. It may be significant that the curve showing the frequency of ovulations in the '0 corpus albicans' group of primiparous females closely parallels the hypothetical curve showing the rate of increase of day length with migration. The small percentage of ovulations in April (2·5%), which is unexpected on theoretical grounds, is possibly attributable to the working of an inherent cycle and also to the effect of individual variations in the rate of foetal growth on the estimated frequency of pairing (see p. 403). The small percentage of successful ovulations in October and November may perhaps be attributed to this effect, and partly perhaps to animals which experience increasing day lengths only on arrival at the breeding zone (see next paragraph). Similarly 95% of successful pairings at the second ovulation are estimated to take place in the 5 months May–September.

Animals migrating north before May will experience decreasing day lengths on migration. Then, if they remain in any one latitude zone, they will continue to experience decreasing day lengths until the end of June, when day length will increase again. Animals which migrate northwards after September (which are unlikely to be more than a very small fraction of the population) will experience decreasing day lengths on migration, and then increasing day lengths on arriving at say 20° S., the rate of increase decreasing until December, after which they will again be subject to decreasing day lengths. By far the greatest change in day lengths occurs during the migratory phase.

According to this hypothesis animals approaching the age of puberty, which migrate northwards at such a time or at such an age that the postulated 'threshold of stimulation' is not quite attained (see p. 422) should not attain puberty until they are next subjected to increasing day lengths. For the great majority, if not all, of these animals this will be during the next southward migration to the feeding grounds. Animals migrating southwards in the 6 months from September to February (which includes almost all individuals) will be subjected to increasing day lengths, and animals making this migration in November will experience the greatest change in day length. It is again significant that the incidence of recent ovulations in nulliparous females in antarctic waters appears to be highest in November and December, falling to zero in March and April (Text-fig. 40). It has also been shown above that animals taken with corpora lutea of ovulation in the ovaries have only recently completed the southward migration.

So far only the influence of light has been considered, but the effects of seasonal feeding and temperature changes are probably also important. Thus, a period of heavy feeding precedes the northward migration and undoubtedly influences the time of puberty. These factors will be discussed again in relation to the adult reproductive cycle. There may also be other less obvious influences at present unsuspected and owing to the lack of precise information about the timing and duration of the migrations of fin whales it is not possible to treat this subject in more detail. It is possible, for instance, that the duration of northward and southward migrations may differ, and the speed of migration no doubt varies for different classes of whales. The curves showing the spread in time of conception may also be less precise than has been assumed, owing to individual variations in foetal growth.

This hypothesis has been developed to show that the observed facts relating to the reproductive cycle at puberty are in close agreement with the two periods of increasing day lengths related to migrations between the breeding and feeding areas. This does not mean that other factors may not influence the timing of the cycle. Thus, in some mammals which have two breeding seasons the first, in the spring, follows a period of increasing day length, and the second follows a period of decreasing day length in the autumn (Eckstein and Zuckerman, 1956). Nevertheless, the thesis that in the fin whale the response to increasing light is the primary exteroceptive factor in the regulation of an inherent sexual cycle appears to be reasonable.

MULTIPAROUS FEMALES

THE PAIRING SEASON AND THE CALVING SEASON

The curve showing the monthly frequency of conceptions of pregnant females in the '0 corpus albicans' and '1 corpus albicans' groups combined is very close to that for females known to be in the first pregnancy by reason of the state of the mammary gland (p. 409, Text-fig. 37). For the purpose of determining the pairing season of multiparous females it is, therefore, assumed that all females with three or more corpora in the ovaries are multiparous. A small proportion of primiparous females will be included in this group since 9% of primiparous females have been found to have three or more corpora lutea and corpora albicantia in the ovaries. This will have a negligible effect on the resulting curve showing the seasonal frequency of pairing.

There are in the material 694 pregnant females which have three or more corpora in the ovaries and for which there are foetal length records. The seasonal frequency of pairing was estimated for this group by relating foetal lengths to the mean curve of foetal growth as was done for all females (p. 403, Text-fig. 31) and for selected groups of newly mature females (p. 412, Text-fig. 37). In this way foetuses have been divided into groups conceived in the periods 12 June–11 July, 12 July–11 August, etc. The estimated frequencies of conceptions in the different monthly periods are set out in Table 17

Table 17. *Estimated frequency of conceptions in multiparous southern hemisphere fin whales, based on 694 records of foetal length*

Period	Conceptions	
	No.	*Percentage*
January/February	0	0·0
February/March	0	0·0
March/April	20	2·9
April/May	164	23·6
May/June	191	27·5
June/July	131	18·8
July/August	63	9·1
August/September	50	7·2
September/October	34	4·9
October/November	24	3·6
November/December	13	1·8
December/January	4	0·6
Total	694	100·0
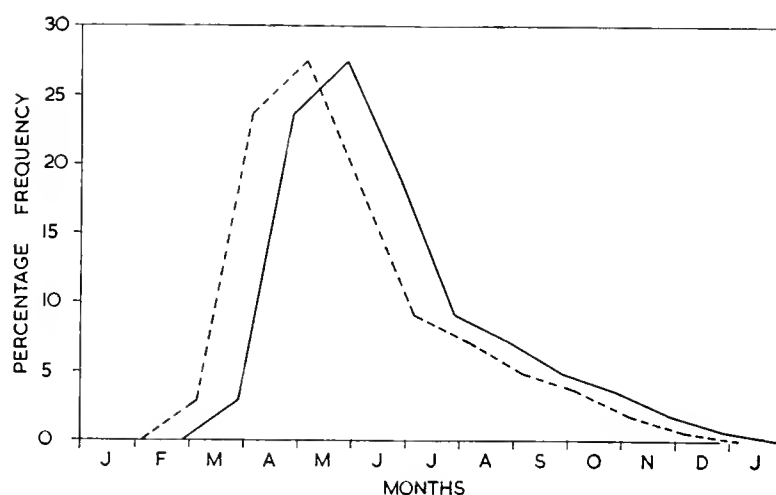
Text-fig. 43. Monthly percentage frequency of pairing (full line) and calving (broken line) of 694 multiparous females (with 3 or more corpora in the ovaries).

and shown graphically in Text-fig. 43. The peak pairing season is from April to July, as opposed to May to September in primiparous females, and the mean date of conception for multiparous females (20 June), is a month in advance of the estimated mean date of conception for primiparous females (21/22 July). The multiparous curve is skewed with a long 'tail' from July to December, whereas the primiparous curve is much more symmetrical about the mean, so it is better to compare the median dates. The median pairing of multiparous females (8 June) is then seen to be about 6 weeks in advance of the median date for primiparous females (21 July). It should also be pointed out that the beginning of the steep rise in the multiparous curve of conceptions is actually about half a month later, that is to say in May, if half-monthly periods are considered. Of the 164 foetuses estimated to have been conceived between 12 April and 11 May, 98 were conceived in the second half of the period, so that only about 90 foetuses were conceived earlier than the beginning of May. These amount to about 13% of all multiparous conceptions.

Evidence given above suggests that the majority of females, if not all, experience a monoestrous cycle in their first sexual season. There is unfortunately very little information on this point for multiparous females. F. D. Ommanney and A. H. Laurie, who examined whales at Durban, South

Africa in June, July and August 1930, recorded details of 16 mature female fin whales. Of these, two were 'resting' but had large maturing follicles up to 5 cm., one was lactating and two were pregnant. Eight had recently ovulated and another probably had recently ovulated; no embryos were found. Two had recent corpora lutea in the ovaries, but it was not possible to ascertain whether they were pregnant or not.

The two 'resting' females and the eight or nine whales which had recently ovulated were probably migrating northwards. The appearance and size of the other corpora in these ovaries suggests that in each case these represent either monoestrous cycles or the *first* of a series of dioestrous cycles. They had not been preceded by recent unsuccessful ovulations. The average size of the largest follicle in these females was only 3·7 cm., which is very similar to the average maximum follicle size (3·8 ± 0·53 cm.)
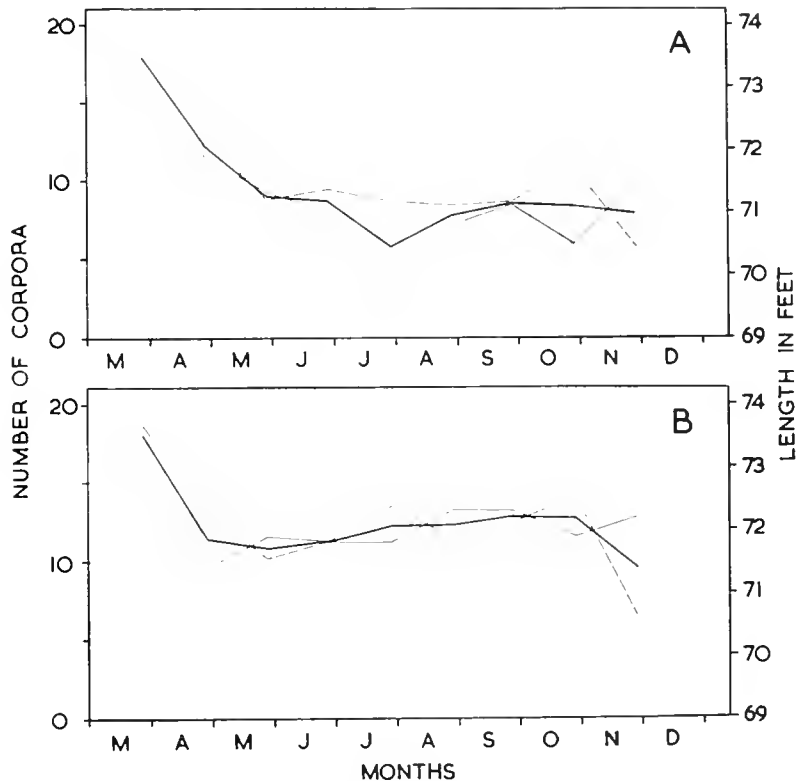
Text-fig. 44. Relation between month of conception and maternal age. Thin line, mean body length; thick line, resultant; broken line, mean number of corpora. A, all pregnant females; B, multiparous females.

in the 'recently ovulated' group from antarctic waters (p. 348). This close agreement suggests that the follicles are not maturing in preparation for a subsequent ovulation, but may be regressing following the current ovulation. It is interesting that three of the recently ovulated females examined at Durban had experienced multiple ovulations.

This material, while not providing very strong support for the thesis of monoestrous cycles, does not contradict it.

The multiparous group may contain some 40 year classes. It has already been mentioned that the '3 corpora albicantia' group conceptions tend to be earlier than those of the '0, 1 and 2 corpora albicantia' groups. One may ask whether individual females tend to conceive at a slightly earlier date each year so that in general the oldest females are the first to ovulate each breeding season. We are in a position to compare the average ages of females conceiving in each month by using corpora

number and body length as indications of age. These two characters are shown in Table 18 and have been plotted in Text-fig. 44. The 'resultant' of these two curves gives a smoothed relative age distribution (thick line).

In the upper graph all sexually mature females are included. The mean age is highest for the mothers of foetuses conceived in March/April, declines through April/May conceptions and levels off in later months. The mothers of foetuses conceived in the July/August period appear to have the lowest average age, though this is perhaps unduly depressed by the low average length for this month. D'Arcy Thompson (1952, p. 175) found a correlation between the size of the mother and the size of the foetus in a sample from a given month, and remarked that this suggested a very considerable growth of the mother during pregnancy. This correlation should, however, be found if, as has been shown above, the older and larger females tend to conceive at an earlier date than younger, and in general smaller, females. In any one month the foetuses of these older females would tend to be older, and therefore larger than those of young females.

Table 18. *Relation between time of conception and maternal age (as expressed by corpora numbers and body length)*

Period of conception	March/ April	April/ May	May/ June	June/ July	July/ August	August/ September	September/ October	October/ November	November/ December
All pregnant females									
Mean no. of corpora	18·7	12·9	8·8	9·4	8·7	8·4	8·6	10·9	5·8
Mean length (ft.)	73·3	71·9	71·3	71·0	69·7	70·8	71·1	70·5	71·5
Sample size	20	170	223	159	101	73	48	32	15
Pregnant females with 3 or more corpora									
Mean no. of corpora	18·7	13·3	10·2	11·3	13·5	11·4	12·5	14·1	6·6
Mean length (ft.)	73·3	71·4	71·9	71·8	71·8	72·3	72·3	71·9	72·2
Sample size	20	164	191	131	63	50	34	24	13

In the lower graph primiparous females are excluded by omitting the 'o and 1 corpora albicantia' groups from the calculations. The average age of females conceiving in March/April is again the highest, but from May onwards the average age per conception month is more or less unchanged, although there is a tendency for the average age to increase slightly up to September and October. The November sample is small.

We may conclude then that for multiparous females in general age does not influence the time at which conception occurs, although in the oldest females this appears to be important. Those which mate in March and April are much older than those females which pair in later months. This point will be of some importance when we come to consider the role of light as an exteroceptive factor controlling the sexual cycle of multiparous females (p. 450).

The average duration of the gestation period is about $11\frac{1}{4}$ months and a curve showing the seasonal distribution of calving has therefore been constructed by advancing the curve of conceptions by three weeks (Text-fig. 43). This assumes that the rate of pre-natal mortality is the same for all foetuses whatever the month of conception. It has been shown that the month of conception is partly related to maternal age, but we do not know whether there are differential pre-natal mortality rates related to maternal age. This factor may influence the shape of the estimated curve of conception frequencies but probably not appreciably, and Text-fig. 43 is thought to give a good idea of the frequency of births, which reaches a peak in April/May.

Post-partum heat

It has not been possible to study post-partum females directly, and we are again restricted to drawing inferences from material collected in the Antarctic. Events during lactation are difficult to establish, because lactating whales are now protected and therefore appear in the catches each year only in small numbers. The present material includes 129 lactating female fin whales examined at South Georgia (in earlier years) and on the pelagic whaling grounds.

Females simultaneously pregnant and lactating

For several Balaenopterid species there are records of females which are simultaneously pregnant and lactating. This appears to be of most common occurrence in the minke whale. Jonsgård (1951) found that in this species lactating females were invariably pregnant, and only 4·5% of mature females were neither pregnant nor lactating. Omura and Sakiura (1956) also concluded that the majority of minke whales in Japanese waters become pregnant as a result of a post-partum ovulation. Chittleborough (1958) gives data obtained by Norwegian workers on the incidence of pregnancy in lactating hump-back whales and Symons and Weston (1958) give a few more records. In this combined sample there are 23 lactating females of which nine, or 39% were simultaneously pregnant. Chittleborough also points out that there are very few females in the resting condition. There appear to be no published records of blue whales which were simultaneously pregnant and lactating, but there are in the records of the National Institute of Oceanography references to two female blue whales which were pregnant while lactating. This is evidently a very rare condition in the blue whale.

As regards the fin whale Hinton (1925, p. 124) refers to four fin whales which were simultaneously lactating and pregnant, and Mackintosh and Wheeler (1929) stated that, although there were a few records of lactating females which were pregnant, none of the lactating whales examined by 'Discovery' Investigations at South Georgia was concurrently pregnant. They concluded that such cases are extremely rare, but 'might arise if a female were impregnated near the end of a long period of lactation' (p. 431). Wheeler (1930, p. 414) stated that seven out of 199 pregnant whales were also lactating, and suggested that a post-partum ovulation may sometimes take place. In later seasons, as we shall see, about one-fifth of lactating females examined at South Georgia were found to be simultaneously pregnant, and Mackintosh (1942, p. 224) stated that there was some evidence that 'the occurrence of whales simultaneously pregnant and lactating is also less rare than in former years'. Ruud (1945, p. 58) remarked that 'nursing females with a foetus seem to be unknown', and Brinkmann (1948, p. 36) gave details of a lactating fin whale with a 77-cm. foetus. He drew attention to the fact that no such case had, so far as was known, been previously recorded. This appears to be the first detailed record to be published, although at that time at least ten such females had been examined by 'Discovery' Investigations (Table 19).

There are in the present material 129 lactating female fin whales examined between 1925 and 1958. Of these 15, or 11·6% were simultaneously lactating and pregnant (Table 19). This material has been subdivided into four groups, the first two representing the work of 'Discovery' Investigations at South Georgia and the next groups representing the work undertaken by 'Discovery' Investigations and the National Institute of Oceanography in pelagic expeditions.

Some explanation of the meaning of this grouping is called for. At South Georgia up to the end of the 1926/27 season, no lactating female had been recorded which was also known to be pregnant. In January 1928 the first female which was simultaneously lactating and pregnant was recorded and following this a much higher number of such females were found amounting to some 20% of all lactating females examined. In the pelagic operations no females pregnant while lactating were found

in 1939/40 and 1940/41, nor in the early post-war years, but in 1953/54 of four lactating females examined two were found to be simultaneously pregnant, and in subsequent seasons a further three were recorded.

It is often said that females cannot be pregnant and suckling a calf at the same time, and the presence of milk has been explained as a premature development of the gland. The Scientific Subcommittee of the International Whaling Commission recently found it necessary to state that 'pregnant whales can be simultaneously lactating and accompanied by a calf' (International Commission on Whaling, Seventh Report of the Commission, 1956. Appendix IV, Report of the Scientific Subcommittee, p. 22). Chittleborough (1958, p. 15) also suggests that lactation may be overlooked in pregnant females. It seems probable that lactation was overlooked in pregnant females in the pelagic samples up to 1952. At South Georgia in 1925–28, however, there was probably a real absence of lactating pregnant females (see p. 459).

Table 19. *Proportion of lactating females which are simultaneously pregnant or recently ovulated*

Samples	Total lactating	Lactating only	Lactating and pregnant		Lactating and ovulation	
			No.	Percentage	No.	Percentage*
South Georgia						
1925–28	21	20	1	4·8	0	0
1928–31	46	36	9	19·6	1	2·7
Pelagic						
1939–52	30	29	0	0	1	3·3
1953–58	32	24	5	15·6	3	11·1

* Percentage calculated from columns 2 and 5 only, because lactating and pregnant females do not ovulate.

If we accept this explanation then the figure of 11·6% for the proportion of lactating female fin whales which are pregnant is too low. A more realistic figure is obtained if we eliminate the data which are thought to be unrepresentative, and use only those from 1928–31 and 1953–58. In this reduced sample there are 78 lactating females, of which 14, or 17·9%, are simultaneously pregnant. The standard error of this percentage is 4·34, which means that the true percentage of lactating females which are simultaneously pregnant probably lies between 9·2 and 26·6%. It is unfortunate that the small size of the sample does not permit a closer estimate than this. It must also be pointed out that the proportion of lactating females which become pregnant may vary from year to year and may increase in response to exploitation. A discussion of the incidence of corpora lutea of ovulation in lactating females will be postponed until the next section (on the post-lactation ovulation) for reasons which will then be apparent.

For the 15 lactating females which were pregnant the foetal lengths are known. They range from 0·31 to 4·4 m.; two-thirds of them are between 1 and 2 m. in length, and the mean foetal length is 1·71 m., corresponding to a foetal age of 7 months. Mackintosh and Wheeler (1929), on the basis of an examination of the sizes of calves and growth of the baleen, concluded that lactation lasts for 6 or 7 months; it is also shown below on other grounds that the calf is suckled for about 7 months. The foetuses of females which are lactating must, therefore, have been conceived at a post-partum ovulation.

Evidence from the sizes of corpora albicantia

Almost a fifth of lactating female fin whales appear to be pregnant as a result of a post-partum ovulation. The question now arises whether only about one-fifth of mature females experience a post-partum heat, or whether the majority of mature females experience a post-partum heat, but only about one in five become pregnant, possibly owing to low fertility at this stage of the cycle.

It will be remembered that there is a group of recently mature females in the first lactation or post-

lactation stages of the sexual cycle which have ovulated once only (Table 15). Thus in the first lactation period a substantial proportion of females do not experience a post-partum ovulation, and in these females there is only one corpus albicans, derived from the former corpus luteum of pregnancy. This suggests that the first of the two postulates in the previous paragraph, namely that only a small proportion of females experience a post-partum heat, is correct. It is, however, possible that the sexual cycle of primiparous females differs in this respect from that of multiparous females (i.e. that they are less fertile) and the evidence now to be presented suggests that this is so and that the majority of multiparous females experience a post-partum heat.

This evidence concerns first, the sizes of corpora in the ovaries of lactating, 'resting' and pregnant females, and secondly, the morphology and histology of certain corpora in the ovaries of lactating females.

Measurements of corpora diameters made at South Georgia between 1925 and 1931 comprise the only consistent series which contains a fairly large number of lactating females. The methods of measurement adopted by later workers vary, and since the methods were standardized in 1954 only a relatively small number (32) of lactating females have been examined. Although the pelagic data nearly double the size of the sample they also increase the variability, and only the South Georgia material is used in the following discussion. Females which are simultaneously lactating and pregnant are not included, for obvious reasons, and the remainder of the females for which corpora measurements are available have been split into three groups according to whether they are pregnant, lactating, or 'resting'. The frequency distributions of the diameters of the largest, second largest, third largest, …up to the sixth largest corpora albicantia, have been obtained. From these the mean diameters and standard errors have been calculated and are shown in Table 20.

Table 20. *Mean diameter* ± 2 S.E. *of corpus luteum and six largest corpora albicantia in the ovaries of 201 pregnant, 48 lactating and 59 'resting' females. The size of the corpus luteum is based upon a much larger sample* (p. 356)

Sexual condition	Corpus luteum	Corpora albicantia					
		1	2	3	4	5	6
Pregnant	11·44 ± 0·15	5·04 ± 0·13	4·05 ± 0·11	3·59 ± 0·11	3·43 ± 0·13	3·13 ± 0·19	3·01 ± 0·20
Lactating	—	5·58 ± 0·20	4·33 ± 0·22	4·15 ± 0·18	3·36 ± 0·20	3·28 ± 0·31	3·00 ± 0·53
'Resting'	—	5·57 ± 0·26	4·42 ± 0·22	3·98 ± 0·24	3·62 ± 0·20	3·20 ± 0·20	3·10 ± 0·31

In Text-fig. 45 the results are presented graphically and each group has been plotted twice so as to cover two reproductive cycles, or four years. It should be noted that this represents the average reproductive pattern. Some of the pregnant group will, however, be animals which conceived as a result of a post-partum ovulation, and therefore did not pass through the lactating and resting stages before becoming pregnant as in the majority of cases. Furthermore, the group of resting females includes some which have recently ovulated (see below, p. 436) and have a young corpus albicans in the early rapid phase of regression, while in others this most recently formed corpus albicans has undergone a much longer period of regression. These variations are a complication in the interpretation of the size distribution of corpora albicantia in this group.

One assumption is made, that with increasing age the corpus albicans progressively shrinks in size. Consequently, if say the third largest corpus albicans in one group is larger than the third largest corpus in the preceding group then the former cannot have been derived from the latter. Similarly, if these two corpora are equal in size then one is unlikely to have been derived from the other because it should have regressed by an appreciable amount in the intervening months. It is necessary again to emphasize that the corpus luteum of pregnancy in the fin whale is much larger than the corpus luteum of ovulation (11·44 cm. as compared with 8·28 cm.). Therefore, among corpora albicantia of

similar age, those derived from corpora lutea of pregnancy should be larger on average than those which are products of the regression of corpora lutea of ovulation.

Let us now attempt to trace the regression of corpora albicantia through successive phases of the sexual cycle. The lines joining corpora in Text-fig. 45 present the conclusions; corpora known or presumed to be derived from pregnancy corpora lutea are shown as black rectangles (shaded in the case of resting females), and those presumed to represent ovulations are shown as white rectangles. The evidence on which these conclusions are based is as follows.
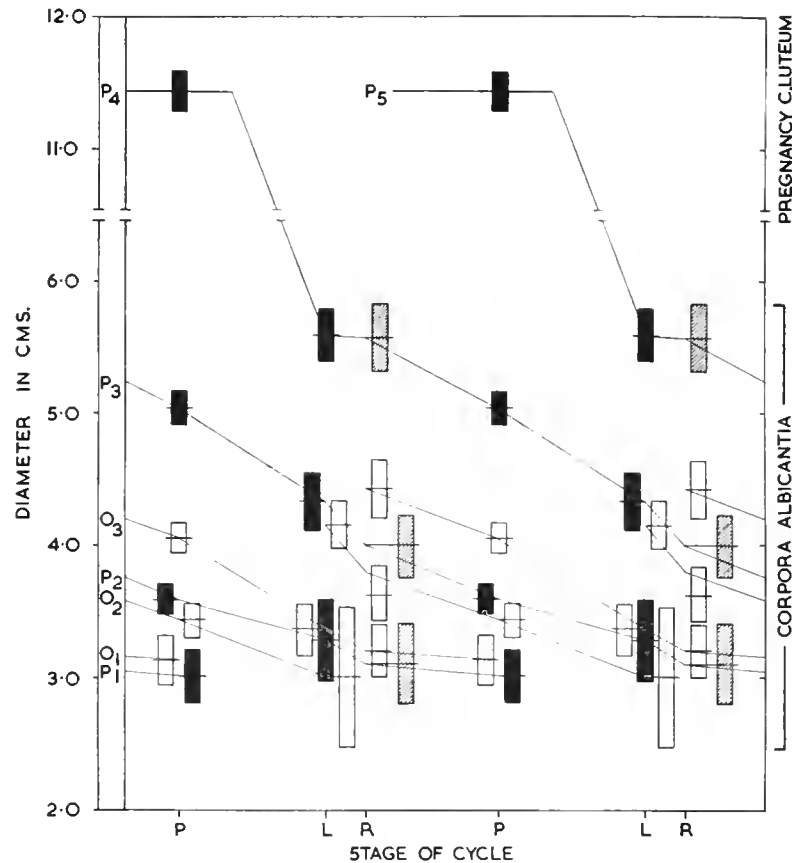
Text-fig. 45. Mean diameters ± 2 S.E. of corpus luteum, and six largest corpora albicantia of pregnant, lactating[1], and 'resting' females plotted to a time scale so as to represent two sexual cycles. See text for explanation.

The mean size of the largest corpus albicans in lactating females is 5·58 cm.; the mean size of the largest corpus albicans in lactating females which are also pregnant (not given in Table 20) is 5·61 cm., and in 'resting' females it is 5·57 cm. These mean sizes are not significantly different, and if we suppose that there has been not more than one post-partum ovulation in lactating pregnant females, then their largest corpus albicans must represent the corpus luteum of the previous pregnancy. The largest corpus albicans in non-pregnant lactating females and resting females is presumed (because of its closely similar size) also to represent the previous corpus luteum of pregnancy.

In pregnant females the largest corpus albicans must either represent the corpus luteum of the previous pregnancy, or an unsuccessful ovulation before the current pregnancy. The latter case is unlikely, because it would mean that the second largest corpus albicans of pregnant females represents the largest corpus albicans of resting females, and has undergone rapid regression. It would also mean that the fin whale is polyoestrous, with on average two ovulations in the breeding season, the second of which leads to pregnancy, whereas the evidence points to a seasonally monoestrous cycle.

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[1] The lactating females are in late lactation (p. 445), so close to the resting stage.

Moreover, if the species were polyoestrous, then in pregnant females the corpus albicans derived from the corpus luteum of the previous pregnancy, in which regression should now be proceeding at a much slower rate than at the beginning of regression, would then appear to have undergone much greater shrinkage than a young corpus albicans from the first of the hypothetical two recent dioestrous cycles. In fact the ovulation which preceded that which led to the current pregnancy almost certainly occurred at the beginning of the resting period, and is probably represented by the second largest corpus albicans in pregnant females (see below).

Now, if there is no post-partum ovulation in the majority of females and if those which do have a post-partum heat usually become pregnant as a result, the second largest corpus albicans of non-pregnant, lactating females should represent the further regression of the largest corpus albicans in pregnant females. This also gives an acceptable rate of regression.

The third largest corpus albicans of lactating females should then be derived from the third largest corpus of pregnant females (that is, the second largest corpus albicans, since the largest corpus is the corpus luteum). It will be apparent from the figure that this is unlikely. The mean size of the third largest corpus albicans of lactating females is actually about 1 mm. greater than that of the third largest corpus of pregnant females and, taking into account the 95% confidence limits, the maximum probable rate of regression would be less than 2 mm. over a period of about 11 months. This is much too slow, and we must conclude that the third largest corpus albicans in lactating females is the product of the regression of an ovulation in the period between parturition and the latter part of the lactation period. As we know that lactating females which are pregnant must have conceived at a post-partum ovulation, it is probable that this third largest corpus albicans of non-pregnant lactating females also represents a post-partum ovulation. In seven months it is presumed to have decreased in diameter by 50% (on average from 8·28 to 4·15 cm.) and in volume by about 87% (Text-fig. 8). This compares with a decrease in the diameter of the regressing corpus luteum of pregnancy of 51% (11·44 to 5·58 cm.) and a decrease in volume of about 88%, over a slightly longer period. This close agreement between observed and inferred rates of regression strongly supports the conclusion that post-partum oestrus is a regular feature in the sexual cycle of the majority, if not of all multiparous fin whale females.

The fourth largest corpus albicans of lactating females is, therefore, likely to be derived from the second largest corpus albicans of pregnant females, and this gives a reasonable amount of shrinkage (about 7 mm. in diameter), associated with regression over about 11 months.

Let us now consider the resting females. Although this anticipates the next part of this paper, it is more convenient to complete this discussion of the regression of corpora before turning to other points. It has been shown that the largest corpus albicans in lactating females represents the former corpus luteum of pregnancy, and it has been suggested that this is also the derivation of the largest corpus in resting females. In the next section it is shown that the group of resting females includes some which have recently ovulated, the ovaries containing an active corpus luteum, or a body partly resembling a corpus luteum and partly a corpus albicans; and others with a very large recent corpus albicans. In this group the largest corpus albicans in some individuals will represent the former corpus luteum, with a mean size slightly less than the largest corpus albicans in lactating females; in other 'resting' individuals the largest corpus albicans will be the product of a recent post-lactation ovulation. Similarly, the size frequency distribution of the second largest corpus albicans in resting females will include some which represent the previous corpus luteum of pregnancy, and some which are derived from a recent ovulation. The effect of this should be to make the largest corpus albicans larger, and the second largest corpus albicans smaller, than they should be when regression of the recently formed corpus albicans is more advanced. In pregnant females there is no recently formed corpus albicans, and the expected separation between the second and third largest corpora albicantia is found.

The second largest corpus albicans in resting females, therefore, represents a recent ovulation at the beginning of the resting period (see below, p. 436, for other evidence of this ovulatory period), which should have a mean diameter larger by probably about 1–2 mm. (The largest corpus albicans in resting females appears to be approximately 1–2 mm. larger than expected by comparison with the largest corpus in lactating females.) The third and fourth largest corpora are then seen to be derived from the second and third largest corpora of lactating females, and become in turn the third and fourth largest corpora albicantia of pregnant females, when they again show a relatively close size grouping as do the second and third corpora of lactating females. Only in the fourth largest corpus albicans in resting females has the line indicating regression not been drawn to the mean, but it is within the 95% confidence limits. In all other corpora groups the suggested regression lines are drawn through the means, and give a consistent picture of rates of regression in size.

The second largest corpus albicans of pregnant females is now seen to be derived from the second largest corpus albicans in resting females. If this resulted from an ovulation at the beginning of the resting period, then it has decreased in size from 8·28 cm. in diameter to 4·05 cm. in about a year (from the beginning of the resting period to the eighth month of pregnancy), that is by 51%. This is not in close agreement with the estimated average percentage shrinkage of corpus luteum of pregnancy (51%), and post-partum corpus luteum of ovulation (50%), over a shorter period of time. It is possible that the size regression of corpora albicantia is slower during pregnancy than during the lactation or resting phases of the cycle. This is borne out by the regression in size of the largest corpus albicans in primiparous females (which will represent an ovulation). When plotted according to the time-scale established for foetal length, this declines from 5·3 cm. at the beginning of pregnancy to about 4·1 cm. at term, and would explain the apparent discrepancy noted above.

A further point to be made is the relation of the fourth largest corpus albicans in resting females to corpora albicantia in other groups. If we assume, for the purpose of the argument, that there is no post-lactation ovulation in the fin whale, then the second and third corpora albicantia of resting females should be derived from the second and third corpora albicantia of lactating females. This means that the fourth largest corpus albicans of resting females does not fit into the pattern nearly so well; its mean diameter is 3·62 cm., larger than the size of the fourth corpus albicans of lactating females (3·36 cm.), from which it should be derived according to this hypothesis. Together with the independent evidence to be described below (p. 436) this indicates that a post-lactation ovulation is a regular feature of the fin whale cycle.

Anomalous corpora albicantia of lactating females

Four lactating females were examined in 1953/54. Of these, two were simultaneously pregnant, and one (no. 1717) was primiparous with one corpus albicans representing the previous corpus luteum of pregnancy. The fourth (no. 636), which was the only normal multiparous lactating female examined, had 15 corpora albicantia in the ovaries, the largest of which was of the usual type, measuring 3·7 cm. in mean diameter, and probably represented the previous corpus luteum of pregnancy. It was similar in appearance to the single corpus albicans in no. 1717, and to the corpora albicantia in other primiparous lactating females examined later. There was one anomalous corpus albicans in the ovaries of no. 636, of a type which had not previously been observed in non-lactating females (Text-fig. 46b). This measured 3·4 cm. in mean diameter.

Subsequently, a further 18 non-pregnant lactating females and two pregnant lactating females were examined. The corpora albicantia in the four pregnant lactating females were all of the normal type, but of the 18 'lactating only' females (excluding two primiparous females with only one corpus albicans of the normal type) nine, or 50%, possessed one of the anomalous corpora.

This type of corpus albicans is found exclusively in lactating females and differs from the more usual corpus albicans, both in its morphology and in its histology. The morphology is similar to that of a corpus luteum of ovulation (Text-fig. 5); the mural luteal tissue tends to be thin and usually has a relatively simple folded pattern, and not the very complicated arrangement associated with the full growth and expansion of the corpus luteum. The central connective tissue core is correspondingly simple, and clearly shows its derivation from the original cavity of the collapsed follicle. But the most conspicuous feature is the colouring. This is usually a pale yellow or yellow-buff in colour, as compared with the usually darker brown of the majority of the corpora albicantia. In this respect they are similar to the corpora aberrantia which have been described above (p. 380), and which represent former corpora lutea of ovulation. This gross resemblance is confirmed by the histological appearance.

The difference between this anomalous type of corpus albicans and normal corpora albicantia is best seen in osmic-treated material (Pl. V, fig. 5, cf. Pl. V, fig. 6). In normal corpora albicantia the osmic-staining lipoid material is evenly distributed in the hyaline collagen representing the former glandular tissue, and is in granular form. In the anomalous corpora the lipoid material is usually in the form of discrete globules of varying sizes. Where the globules are large the lipoid material occurs at the periphery after fixation, and surrounds a central vacuole which was presumably fluid-filled
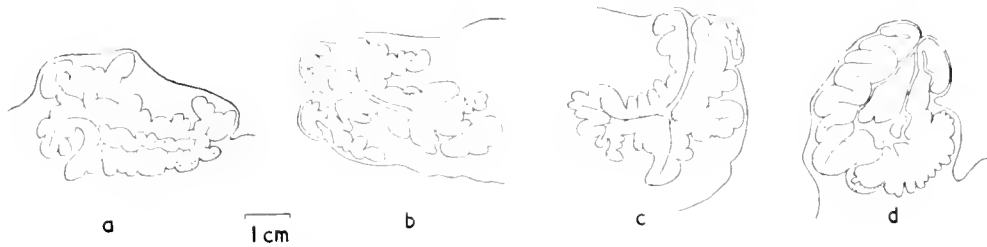
Text-fig. 46. Morphology of anomalous corpora of lactating females.

before treatment. There are also lipoid deposits in granular form as in the normal type of corpus albicans, and these granules are more abundant in the peripheral parts of the corpus. The arrangement of lipoid material around fluid-filled vacuoles is very similar to the condition of some of the corpora aberrantia and atretica (see Pl. VII, figs. 6, 7).

This similarity between the anomalous corpora albicantia of lactating females and the corpora aberrantia and atretica is suggestive, and it is probable that these anomalous corpora represent ovulations during lactation. The relative age of these corpora (as indicated by the amount of vascularization for instance) appears to be very similar to the age of normal 'young' corpora albicantia, from which they differ mainly in the arrangement of the lipoid material. In view of this they do not represent recent ovulations, towards the end of lactation, but probably are the products of post-partum ovulations.

The mean diameter of nine of these anomalous corpora was 3·8 cm. Considering the small size of the sample, and the fact that the method of measuring may be slightly different, this is quite close to the mean size of the third largest corpus (4·15 cm.) in the sample of lactating females from South Georgia, which on other grounds was assumed to be from a post-partum ovulation. In the period of approximately seven months since its formation it had regressed by 51 % in diameter, which was shown to be in close agreement with the rate of regression of the former corpus luteum of pregnancy during lactation.

About 18% of lactating females are simultaneously pregnant, and of the remaining lactating females about half are presumed (on histological grounds) to have experienced a post-partum ovulation. Combining these data suggests that at least 60% of multiparous females experience a post-partum ovulation. No allowance has been made for the possible variance of these small samples, which is particularly large in respect of the incidence of anomalous corpora.

These anomalous corpora are very similar histologically to the corpora aberrantia described above (p. 380), but in size and gross morphology resemble normal corpora albicantia more closely. Like the corpora aberrantia they probably represent former corpora lutea of ovulation which have undergone an aberrant type of regression. Not all corpora lutea of ovulation undergo this type of regression. Nulliparous females, for instance, usually have normal 'young' corpora albicantia which cannot certainly be distinguished from the single corpus albicans in primiparous lactating or resting females.

Thus, it seems likely that more than two-thirds of multiparous females, possibly all, experience a post-partum ovulation. Indeed, the size distribution of corpora described above could not be expected to show such a clear pattern if only two-thirds of females experience a post-partum ovulation. In primiparous females, however, there is evidence that a substantial number do not have a post-partum ovulation.

Ovulation after abortion, stillbirth, or loss of calf

Chittleborough (1958) has examined six female humpback whales which showed anatomical evidence of a recent birth, but in which the mammary gland was involuting, suggesting that the calf had been lost at, or just after, birth. In five of these ovarian activity had recommenced; in three cases mature follicles were present; in another ovulation had just occurred and in the fifth a developing corpus luteum indicated a recent ovulation. This is compatible with a normal post-partum ovulation since these calves were presumably very young, and a post-partum ovulation seems to be a not uncommon feature of the sexual cycle of the female humpback whale.

As regards the possibility of ovulation after the premature termination of pregnancy, another of Chittleborough's observations is of interest. One of over seventy female humpback whales in late pregnancy had a regressing corpus luteum and one mature follicle 4·8 cm. in diameter. This suggests that the initiation of pro-oestrus changes is dependent on the regression of the corpus luteum of pregnancy. It is unlikely that the fin whale is different in this respect. A further possibility is that ovulation might closely follow abortion or foetal death in mid-pregnancy if this is also associated with regression of the corpus luteum of pregnancy. It has been shown that there is a follicular cycle during pregnancy in fin whales, with peak activity corresponding to a foetal length of 1–2 m. (p. 348). The follicles enlarge at this time, but maturation and ovulation are suppressed owing to the presence of an active corpus luteum. If for any reason, such as an abortion or foetal death, the corpus luteum ceased to be functional at this stage of the cycle it might no longer suppress follicular maturation, and ovulation might follow.

Kimura (1957) reports on a case of fin whale triplets in which two (measuring 19 ft. 8 in. and 15 ft. 0 in.) were necrotic and one (5 ft. 2 in.) was normal. This would seem to be a case of foetal death of twins, followed by a further ovulation which initiated a second pregnancy, but it is not possible to say what was the interval between the death of the twins and the new conception. It may have been quite short, but alternatively the further ovulation may have been delayed until the next ovulatory period. The latter would seem to be the more probable sequence.

We may conclude that the loss of a near-term foetus, a stillbirth, or the loss of a young calf, will probably be followed by an oestrous cycle comparable with normal post-partum heat. The termination of pregnancy by foetal death or abortion at an earlier stage will most likely be followed by ovulation at the next ovulatory period.

Post-lactation heat

In the humpback whale the lactation period lasts $10\frac{1}{2}$ months, weaning occurs on average at the end of June and the majority of females are in oestrus between July and September, with pro-oestrus most common in July. The female is not usually in anoestrus after lactation, and in some cases there is

a recrudescence of ovarian activity before the end of lactation. Chittleborough (1958), found that in this species 18% of females in late lactation had maturing follicles or had recently ovulated.

In the fin whale the lactation period is shorter, and weaning probably occurs on average in December (see below, p. 446); pairings are not frequent until May. There is, however, strong evidence to show that, as in the humpback whale, there is an ovulatory period just after lactation, and that some females may undergo oestrous changes and ovulate in late lactation. Some 20% of female fin whales in late lactation have maturing follicles in the ovaries (over 3 cm. in diameter (Text-fig. 4)), and some 5% (4·6±4·2) of lactating females have recently ovulated, as evidenced by the presence of a corpus luteum of ovulation in the ovaries (Table 19). This is in close agreement with Chittleborough's findings in late-lactation humpback whales.

The majority of lactating fin whales found in antarctic waters are in late lactation, and are very near to the time of weaning. This is discussed in more detail in the next section (p. 445). The evidence as to the size of the calf at weaning, the foetal age in pregnant lactating females, and the lower incidence of diatom infection, all points to this conclusion.

As Mackintosh and Wheeler (1929) showed, the period of lactation is succeeded by a 'resting' period of anoestrus which lasts until the following winter. However, when we examine the records for females taken in the Antarctic which are neither lactating nor pregnant, and which should, therefore, be in the 'resting' condition, we find that a proportion of them have recently ovulated. So as to minimize the possibility of including pregnant females (perhaps with small foetuses, or aborted foetuses) in this sample, the material on which the following discussion is based is restricted to whales which were examined personally by the biologists. Where a corpus luteum was seen but no foetus or embryo was found the uterus was searched. Although some females in early pregnancy may be included in this sample, their numbers must be very small.

The greatest numbers of recent ovulations are recorded from January (Table 22), a month in which it is estimated that very few conceptions occur (Text-fig. 31). Apart from the care taken to include only those females in which it is reasonably certain that no embryo was present there are two facts which confirm the validity of the sample. The evidence of the mean size of the corpus luteum in these whales, which is significantly smaller than the mean size of the corpus luteum of pregnant females (p. 356), and the mean size of the largest follicle, which is significantly greater than the mean size of the largest follicle of pregnant females (p. 348) confirm that most, if not all, of these recent ovulations are correctly diagnosed.

In the material up to 1958 there are 465 non-pregnant, non-lactating females which fulfil these conditions and of these 59 or 12·7% had recently ovulated before death. This figure needs some adjustment, because the discrepancy between the early period of the investigation at South Georgia and the later seasons suggests that in the early seasons at South Georgia recent ovulations may have been under-represented. Thus, in the four seasons 1924–28, some 55 non-pregnant, non-lactating females are recorded, but no recent ovulations; in the three seasons 1928–31 eight out of 51 such females had a corpus luteum of ovulation in the ovaries (15·7%). If these 55 records are eliminated there are 410 non-pregnant, non-lactating females, of which 59 or 14·4±3·5% are deemed to have had a corpus luteum of ovulation in the ovaries at the time of capture. It makes little difference to the argument below whether or not we restrict the sample in this way. Another fact which should be recalled is that, although the mean size of the largest follicle of 'resting' females is similar to that of lactating females (Text-fig. 4), the maximum follicle size of 'resting' females is 8 cm., only slightly less than the largest follicles in recently ovulated females, whereas the maximum follicle size in the sample of lactating females was about 5 cm. This suggests that some 'resting' females are in an immediately post-oestrus condition. Although there are a number of 'resting' females which have a

corpus albicans in the early stages of regression, occasionally with some yellow glandular tissue remaining, in no case is such a young corpus albicans associated with a corpus luteum of ovulation. This is valid evidence for a monoestrous cycle at this time, as in females at puberty (p. 416).

The records of the incidence of diatom infection show that the ovulation which gives rise to this corpus luteum occurs at about the time of the entry into antarctic waters of the so-called 'resting' females. Diatom infection has been assessed as absent, incipient, moderate, and extensive, and the results are shown for 268 lactating, recently ovulated or 'resting' females in Table 21. Females in which the diatom film is absent or incipient have probably been south of the Antarctic Convergence for a month or less (Hart, 1935). Of lactating females $70.9 \pm 10.5\%$ fell into one or other of these two categories, and of recently ovulated females $71.4 \pm 15.3\%$. In contrast to this low incidence of diatoms in lactating and recently ovulated females, only $46.2 \pm 8.2\%$ of 'resting' females fell into these two categories. This difference is statistically significant at the 95% level.

These figures strongly suggest that this ovulation occurs at or very soon after the end of lactation, and the approximately 5% of lactating females which had recently ovulated presumably represent a premature ovulation at this time as in the humpback whale.

Table 21. *Incidence of diatom infection in three classes of fin whale females*

Diatoms	Lactating		Ovulation		Resting	
	No.	Percentage	No.	Percentage	No.	Percentage
Absent	38	44·2	18	51·4	37	25·2
Incipient	23	26·7	7	20·0	31	21·1
Moderate	13	15·0	6	17·1	30	20·4
Extensive	12	14·0	4	11·4	49	33·3
Total	86	99·9	35	99·9	147	100·0

Table 22. *Monthly frequency of recent ovulations in mature non-pregnant, non-lactating fin whale females (Antarctic)*

	October	November	December	January	February	March	April	Total
Resting	3	10	28	99	97	72	42	351
Ovulations	1	5	10	27	9	7	0	59
Total	4	15	38	126	106	79	42	410
Percentage ovulations	25·0	33·3	26·3	21·4	8·5	8·8	0·0	14·4
2 S.E.	43·2	18·0	14·3	7·3	5·4	6·4	—	3·5

It is now possible to test the hypothesis that female fin whales experience a monoestrous cycle at the time when they are weaning or have just weaned the calf, shortly after entering antarctic waters, by examining the monthly incidence of recent ovulations in the Antarctic. This is set out in Table 22 for a sample of 410 non-pregnant, non-lactating fin whales, taken between October and April over a number of years. The proportion of females with a corpus luteum of ovulation in each month declines from one-third in November to none in April. The standard errors of these percentages have also been calculated, and the results are shown graphically in Text-fig. 47. Owing to the small size of the monthly samples the standard errors are large, and the only samples which show a significant difference in the incidence of ovulations in successive months are those from January and February, March and April. However, when the percentages and standard errors are considered as a whole the decline from November to April cannot be disputed.

A straight line has been fitted to these points by inspection, and extrapolated to give a value for September. The justification for extrapolating for the September value will become apparent during the ensuing discussion. There is, of course, no certainty that a straight line best describes the monthly

incidence of ovulations, and it is possible that a sigmoidal curve, or an irregular curve, as well as giving a better fit, might be nearer to the truth. Calculations have, therefore, also been made using a sigmoid curve to estimate the monthly incidence of ovulations, and also using the actual means of the samples. It makes little difference to the following discussion which fit is adopted, and the straight line shown in Text-fig. 47 is used below, because it probably gives the most likely value for September.

It is supposed that the numbers of fin whales south of the Antarctic Convergence are at a minimum in July and August and then build up to a maximum in say February (see Mackintosh, 1942, p. 270; Mackintosh and Brown, 1956, fig. 2; and evidence from the catch statistics). The numbers of non-pregnant, non-lactating females in the Antarctic will follow a similar pattern though later in time (Text-fig. 48b). According to the hypothesis under consideration, these females ovulate either shortly before or soon after their entry into the Antarctic population. A small proportion of the fin whale population probably overwinters in antarctic waters (Hart, 1935, p. 276; Mackintosh, 1942, p. 250), and it follows that apart from these, all non-pregnant, non-lactating females present in the antarctic
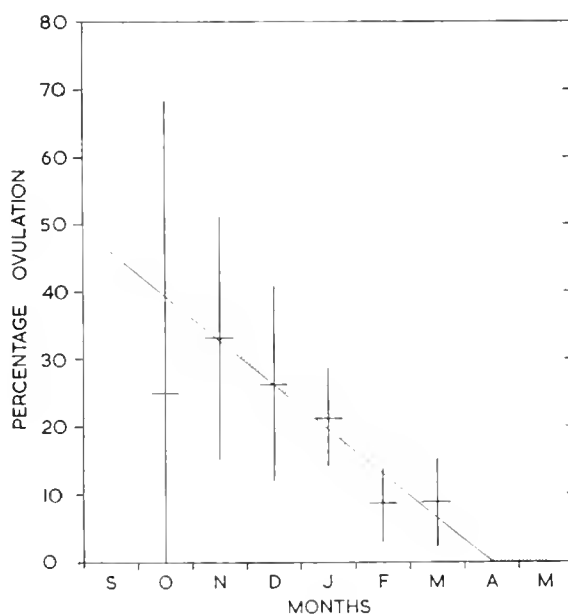
Text-fig. 47. Monthly percentages (± 2 s.e.) of recent ovulations in antarctic waters.

in September should have ovulated recently. In the following months there will be an increasing influx of new arrivals which are expected to ovulate just before, on arrival, or soon after arrival, but in successive months there will also be an increasing accumulation of females which have been in antarctic waters for some time, and have ovulated some time before. It is, therefore, to be expected that the monthly proportion of recent ovulations would decline as the number of truly 'resting' females in the population increases, and this is in fact what the actual figures show.

It has been pointed out that in September all but the small proportion of non-pregnant females which have remained south of the Antarctic Convergence during the winter months, or have migrated into the Antarctic before September, should have recently ovulated. In fact Text-fig. 47 shows less than half of these females to have a corpus luteum of ovulation. So far we have not considered the length of life of the active corpus luteum of the cycle, but this is an important factor which will affect the figures for the incidence of ovulations. Thus, if the corpus luteum persists in a recognizably active form for a month, the figures given in Table 22 and Text-fig. 47 will represent the monthly frequency of ovulation, but if, for example, the corpus luteum persists for only 2 weeks after entry into the whaling grounds, then the observed frequencies of corpora lutea of ovulation must be doubled to give the true

monthly frequency of ovulation. This would give an estimate of 92% for the incidence of ovulations in September, which is probably nearer the true proportion.

The life of the corpus luteum of the cycle as in other mammals is likely to be nearer half a month than a month. Thus, Eckstein (1949, p. 400) remarks that: 'The life span of the c.l. in different species is remarkably uniform and independent of body size. The range of variability encountered is about 10–20 days (the upper limit being represented by the cow), but in the great majority of animals it is probably of the order of only 10–15 days.' Harrison (1948, p. 323) also states that regression begins 10–18 days after ovulation. There is no reason for supposing that pseudo-pregnancy is a feature of the reproductive cycle of whales, and there are several good reasons for supposing that it is not. While definite proof is lacking it is highly probable that the corpus luteum of ovulation in the whale persists in a recognizably active state for a period of between 15 and 20 days.

Table 23. *Monthly percentage of adult females pregnant; South Georgia* 1925–31, *pelagic* 1932–52

Month	South Georgia		Pelagic	
	No.	%	No.	%
September	1	(100·0)	—	—
October	40	85·0	—	—
November	86	77·9	—	—
December	111	82·0	131	79·4
January	134	70·1	336	64·3
February	81	49·4	320	67·8
March	65	32·3	239	51·9
April	30	26·7	72	7·0
May	2	(50·0)	—	—
	550	64·9	1098	60·7

We may now proceed to test the hypothesis concerning this post-lactation ovulation, using some actual figures to compare the cumulative curve of ovulations with the increase in the population of 'resting' females in antarctic waters. The results of these calculations are presented in Table 24 and illustrated in Text-fig. 49.
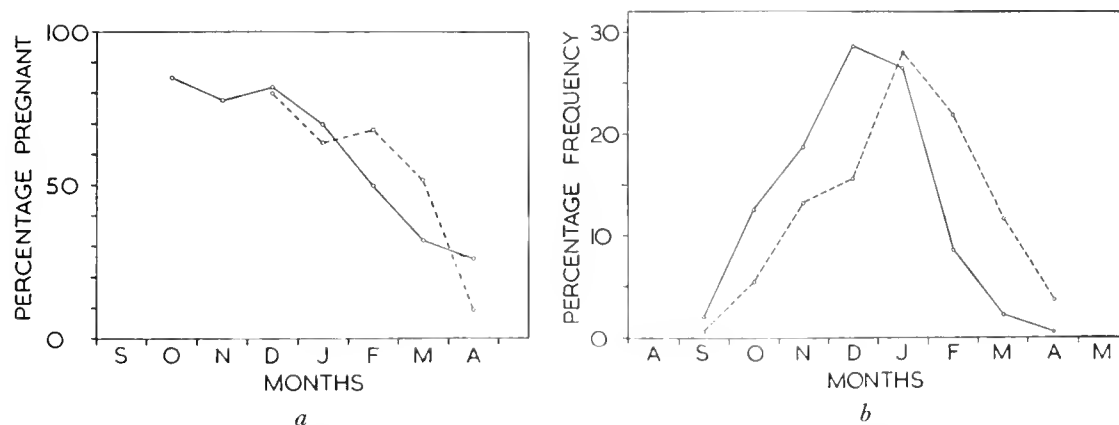
As a basis for the calculations it has been assumed that the catch at South Georgia in the eight seasons 1927–35 gives a reasonably accurate picture of the monthly variation in numbers of the antarctic fin whale population. The figures for the pelagic catch cannot be used, because in recent seasons there have been no catches before December or January; and in earlier years the catches are not considered to be representative of the population present, because of the selection of the more valuable blue whale, so that the earlier months are under-represented (see Mackintosh, 1942). The calculations have been repeated for the eight post-war seasons, 1948–54, 1955–57, at South Georgia (the season 1954–55 being excluded, because it was clearly anomalous with peak catches of fin whales in October and November). The results are similar to those for the earlier period.

The monthly percentage of females in the catch is fairly constant, and on average slightly less than 50%, though it varies between 40–54% (from Mackintosh, 1942, table 25). The catch at South Georgia in 1927–35 is here taken to represent the variation in numbers of females. The monthly percentage of immature females (Table 24, column (2)) is taken from Mackintosh (1942, table 26b), and an arbitrary figure allowed for September. This permits the approximate numbers of mature females to be calculated (column (3)). The monthly percentage of non-pregnant mature females in the catch (shown in column (4)), is obtained from Table 23, Text-fig. 48a and enables the catch of non-pregnant mature females to be estimated (Table 24, Text-fig. 48b). The monthly percentage of

Table 24. *Monthly frequencies of non-pregnant mature females at South Georgia (1927–35) and the estimated cumulative frequencies of ovulations in this class assuming a corpus luteum life of 15 or 20 days. See text for explanation*

| Month	Catch (1)	Percentage immature (2)	No. mature from (1) and (2) (3)	Percentage non-pregnant (4)	No. non-pregnant from (3) and (4) (5)	Percentage ovulations (6)	No. of ovulations from (5) and (6) (7)	c.l.o. 15 days		c.l.o. 20 days	
								No. of ovulations (7) × 2 (8)	Cumulative frequency (9)	No. of ovulations (7) × 1·5 (10)	Cumulative frequency (11)
September	195	(20·0)	156	(10·0)	16	(46)	7	14	14	11	11
October	1348	24·1	1013	15·0	152	40	61	122	136	91	102
November	1930	15·2	1637	22·1	362	33	121	242	378	181	283
December	2919	18·6	2376	18·0	428	26	111	222	600	166	449
January	3714	30·7	2574	29·9	770	20	154	308	908	231	680
February	2136	44·5	1185	50·6	600	13	78	156	1064	117	797
March	879	46·0	475	67·7	322	7	23	46	1110	34	831
April	208	33·3	139	73·3	102	0	0	0	1110	0	831

Text-fig. 48. *a*, Monthly '% pregnant', South Georgia 1925–31 (full line), pelagic 1932–52 (broken line). *b*, Monthly frequency of pregnant (full line) and non-pregnant females (broken line) in the South Georgia catches 1927–35.

recent ovulations (uncorrected for the active life of the corpus luteum), is then obtained as described above (Text-fig. 47), and the number of recent ovulations observed in each month (column (7)) is obtained by applying these percentages to the estimated number of non-pregnant females in the catch. The question of the proportion of lactating whales in the monthly samples is discussed in the next section (p. 448), and it is shown that there are relatively large numbers at South Georgia from December onwards, but that very few enter the pelagic grounds until January or February, having weaned the calf before entering colder waters. Those lactating females which do enter the catches are either about to wean, are weaning, or have just weaned, the calf (see below, p. 445). For present purposes lactating females are, therefore, included in the non-pregnant group. Columns (8) and (10) show the estimated numbers of ovulations on the assumption that the corpus luteum is recognizable as such in females taken on the whaling grounds for 15 or 20 days respectively, and in columns (9) and (11) the cumulative frequencies of recent ovulations are shown.

If we are correct in postulating that new arrivals to the non-pregnant fin whale female population in the Antarctic ovulate and then enter the true 'resting' state, then the cumulative figures for the number of ovulations should correspond to the build-up of the antarctic population of 'resting' females. Unfortunately, we have no data on the actual numbers of animals in the population, but for present purposes we may assume that the monthly catches correspond to the relative abundance in the sea. The catching intensity is probably rather less at the beginning and end of the whaling season, but this does not affect the general argument. In Text-fig. 49 the catch of non-pregnant females is

compared with the estimated cumulative frequencies of ovulations, the upper limit of the shaded portion representing a corpus luteum life of 15 days and the lower representing a life of 20 days. It is apparent that there is a reasonably good correlation between these curves, and a cumulative curve of ovulations may be taken to represent the entry of 'resting' females into the antarctic population.

The best agreement is obtained if the centre of the shaded area, corresponding to a corpus luteum life of 17–18 days, is used. Up to January there is fairly close agreement, but after this the numbers of non-pregnant adult females in South Georgia waters fall off. Probably very small numbers arrive in the Antarctic after March.
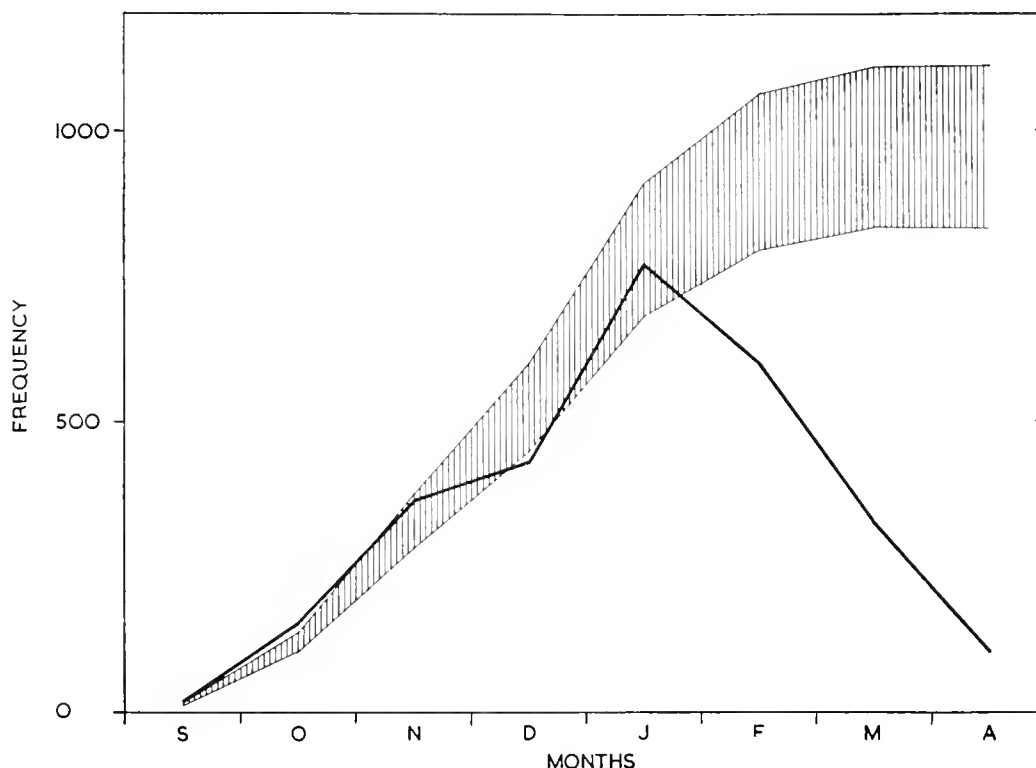
Text-fig. 49. Thick line, catch of non-pregnant females, South Georgia 1927–35, from Text-fig. 48. Shaded area represents estimated cumulative frequency of ovulation for corpus luteum life of 15–20 days. See text for explanation.

According to these calculations 50% of non-pregnant females are south of the Antarctic Convergence by mid-December, and almost all have arrived by the end of March. As regards the true monthly frequency of this summer ovulation, December may, therefore, be considered as the median month. This is in reasonably close agreement with the cycle of ovarian activity in pregnant females, which shows a peak in November/December (see p. 348, Text-fig. 4). Pregnant females enter antarctic waters about a month in advance of non-pregnant females (Text-fig. 48b), and it would seem that in this class also ovarian activity is correlated with the southward migration. It will also be remembered that a similar correlation was demonstrated for some nulliparous females at puberty. We will return to this interesting point later (p. 450).

The main purpose of this brief discussion has been to show that the estimated cumulative frequency of ovulations corresponds fairly closely with the ascending limb of the curve showing the catches of non-pregnant mature fin whale females at South Georgia, and therefore supports the hypothesis put forward above concerning an end-of-lactation, or post-lactation, ovulation. The catch statistics show that the peak in the pelagic catch of fin whales is usually a month later than the peak numbers at South Georgia. This island 'occupies a peculiar position where Antarctic conditions extend into a

comparatively low latitude, and Fin whales may be plentiful there before they have reached the higher latitudes elsewhere. It is not until about the New Year that the big herds of Fin whales make their appearance on the pelagic grounds' (Mackintosh, 1942, p. 272, and his tables 23 and 24). Rayner (1940, p. 261) showed that fin whales marked near Shag Rocks (just west of South Georgia) were not taken by the South Georgia whalers, but some were taken further south on the pelagic grounds. Fin whales marked and recovered on the South Georgia whaling grounds are found to belong to migrating herds which stop to feed in these waters, averaging about 15 days in the area.

Similar calculations may be made, basing them on an arbitrary pelagic population, the monthly frequency curve being similar to that for South Georgia, but attaining peak numbers a little later. There is again close agreement between the ascending limb of this curve and the cumulative frequency of ovulations estimated from it, and the cumulative curve again attains the 50% level just before mid-December.

This hypothesis is not entirely satisfactory in detail. A point which may be raised is that if, as a rule, non-pregnant females ovulate after arriving in antarctic waters, then more cases of very recent ovulations should have been observed, in which the follicle is still in the initial collapsed state, or the corpus luteum is in the initial phases of development (see p. 354, Text-fig. 5 a) and has not filled out. Let us suppose that this initial stage lasts about 8 days as in certain ungulates (Harrison, 1948, p. 315). Then if ovulations occur on the whaling grounds some 44% of observed corpora lutea of ovulation are expected to be in this initial phase. Allowing for the large standard error of this percentage a minimum of 16 out of the 59 corpora lutea recorded should have been in this condition. The very early stages, more easily recognizable to observers, should be proportionately fewer. Since the present investigation began in 1954 only 10 recent ovulations have been recorded, and two of these were in the early stages, with the corpus luteum presenting a folded and unexpanded appearance, the original follicle cavity still being discernible (Text-fig. 5 b). This suggests that they were less than a week old. A number of the early records also note that the corpus luteum looks very young, but fuller details are lacking. It is, therefore, uncertain whether the earliest post-ovulation stages have been observed in antarctic waters, and it is likely that this ovulation usually occurs just before the entry of these females into the whaling grounds. Some 80% of lactating females are believed to wean their calves before they appear on the pelagic grounds (see p. 450).

It is clear that this problem of the precise relationship of the summer ovulatory period to the lactating and 'resting' phases of the sexual cycle is complex. There can, however, be little doubt that in the fin whale there is as a rule an ovulatory period at the end of, or just after, lactation as in the humpback whale. In contrast to the humpback whale, and related to the shorter duration of lactation, this ovulation in the fin whale occurs during or after a southward migration to the Antarctic, instead of being associated with a northward movement to warm waters.

Almost without exception it appears to be an unsuccessful ovulation, but there are a few foetuses estimated to have been conceived at this time, in some cases possibly in antarctic waters (p. 403). There are also a few observations of pairing between baleen whales in polar waters in summer. Nishiwaki and Hayashi (1950) described copulation of two humpback whales in antarctic waters in January, and a similar observation was made from a whale catcher by a British Whaling Inspector (J. E. P. Brass) in December 1934, in 60° S., 95° E. 'I also had the experience of seeing two whales copulating. The pair came to the surface on their sides with flippers securely interlaced' (MS. notes). Unfortunately he gives no details and does not record the species. There are other closely similar, but less reliable accounts by whalers of fin and blue whales seen in coition in antarctic waters. Hinton (1925) refers to reports by whalers of pairing observed in the summer months in the North Atlantic (fin and blue whales off the Finmark coast, pp. 118–19, 141). These accounts strongly suggest that

in Balaenopterids not only oestrus and ovulation, but occasionally mating and conception, may occur in polar waters in the summer months. It would appear that at most only about 6% of all conceptions occur in this way (Table 11, October–March conceptions). This is correlated with the observation that the great majority of male fin whales examined in antarctic waters are found to be in full anoestrus (p. 396).

THE LACTATION PERIOD

Text-fig. 35 (p. 410) illustrates the cycle of activity of the mammary gland. Attention has already been drawn to the relative thinness of the mammary glands of nulliparous and primiparous females, and to the fact that after its expansion during the first lactation period the mammary gland does not return to its former size, but decreases to a depth of about 5 cm. in primiparous 'resting' females and in second-pregnancy females. This figure also suggests that in lactating multiparous females the mammary gland is rather thicker than in primiparous females, although the data are too small to allow definite conclusions to be drawn.

In multiparous females the mammary gland in full lactation averages 20 cm. in depth (range 10–30 cm.); the lobules of glandular tissue with expanded alveoli are large, and the connective tissue is arranged as relatively thin supporting septa. In pregnant females and 'resting' females which have experienced at least one lactation period, the glands are either involuted or intermediate between this condition and the lactating condition. The 'intermediate' glands are then about 7–11 cm. thick, brownish in colour with large lobes of alveolar tissue and relatively small amounts of connective tissue (Mackintosh and Wheeler, 1929, fig. 137). In the involuted mammary gland the brownish alveolar lobes are smaller than in the 'intermediate' gland, and the connective tissue framework is correspondingly more conspicuous (Mackintosh and Wheeler, 1929, fig. 138); the thickness of the gland is usually from 4 to 8 cm. There is little chance of confusing a gland in this condition with an immature gland, because both thickness and colour are usually very different.

Another group is shown in Text-fig. 35, which has been termed the 'end of lactation' group, and some explanation is necessary. Chittleborough (1958) noted that after lactation has ended, when involution of the gland is well-marked, there may be liquid in the lacteal ducts, which is usually a whitish or turbid yellowish thin fluid. There are 22 fin whales in the present material which have mammary glands in this condition. They are considered to be involuting after the successful termination of lactation or following loss of the calf. They range in thickness from 7 to 17 cm. (mean 11·1 cm.) and are shown in Text-fig. 35 as an 'end of lactation' group.

It will be noted that the upper part of the histograms showing mammary gland depth are closely similar in both the 'resting' and pregnant groups of females, and overlap the values for the 'end of lactation' group, and even the two lowest values in the lactating group. This is to be expected in the case of the resting group which normally follow on after weaning; the thicker glands in the pregnant group must similarly be considered to represent females which became pregnant at a post-partum or post-lactation ovulation. The estimated foetal ages for these females agree with this interpretation.

The criterion of lactation adopted here is the presence, in the mammary glands or ducts, of milk which is apparently normal in colour and consistency. Usually the appearance of the cut gland is also diagnostic. The quantity of milk present is not important, because it will vary according to the time elapsed since the calf was last fed. As was noted above the presence of milk is usually, but not invariably, associated with mammary glands which are thicker than those of non-lactating females (Text-fig. 35).

However, the presence of milk or gross appearance of the gland are not completely valid criteria of lactation because some females diagnosed as being in full lactation are found, on histological examination, to have stopped active secretion of milk. Van Lennep and van Utrecht (1953) have shown that of 69 females (mainly blue and fin whales) said on these grounds to be lactating, histological

criteria showed that a substantial proportion were either not lactating or were in a doubtful condition. Chittleborough (1958) has also distinguished on histological grounds two groups of females, each with apparently normal milk in the glands. When the cells lining the alveoli were actively secreting the female was classified as still suckling a calf, but if the lacteal ducts contained milk and the alveolar cells were no longer secreting, then it was considered that 'the female had either recently lost, was weaning, or had just finished weaning the calf, and that the apparently normal milk present in the ducts was a residuum which would shortly have disappeared' (p. 7).

Of the 69 females examined by van Lennep and van Utrecht (1953) four humpback whales and a sperm whale should be excluded from the present discussion because in these species the calf is usually weaned in low latitudes. Of the remaining 64 fin and blue whales, 41 were held to be lactating, six definitely not lactating, and 17 could not be definitely assigned to either of the first two groups. In some of the material in the third group fixation was bad; some of these whales were thought to be weaning the calf; and at least two were thought to be pathological. We are not likely to be far wrong if we assume that about half of the females in the doubtful group were weaning the calf. Then for 41 females known to be lactating there are 14 which are thought to have just ceased to secrete milk, that is about 25%. Even if the doubtful group is excluded, there is a minimum of 6 out of 47 (or 12·8%) which were no longer secreting milk. On the west Australian coast Chittleborough (1958) found 23% (5 out of 22) of female humpback whales with milk in the glands to be in this condition. Lactating females appear in the catches off the west Australian coast shortly before weaning, and the period after secretion has ceased when normal milk is still present in the glands, is almost certainly very short. It is interesting to note that the lactating female fin whales taken in antarctic waters have probably been on the whaling grounds for less than a month, possibly only for 2 weeks. This conclusion receives support from the results of the analysis of the incidence of diatom infection (Table 21). In some 71% of lactating females diatoms are absent or incipient, showing that the majority of lactating females in the sample have entered the Antarctic recently, probably less than a month before their capture (Hart, 1935).

Further support comes from an analysis of the foetal lengths of those lactating females which are also pregnant. The work of Mackintosh and Wheeler (1929) strongly suggested that the lactation period was about 6–7 months, and this estimate cannot be very far out. In fact it is in very close agreement with the conclusions reached below. The average foetal length will give us the average foetal age for this class of females, and will enable us to see how near this group of females is to weaning the calf. It is reasonable to assume that the lactation period is no longer in pregnant lactating females than in non-pregnant lactating females, and that in other respects the behaviour of these two groups is similar.

There are 15 fin whale females in the material which are concurrently pregnant and lactating. The foetal lengths range from 3·1 to 4·4 m. with a mean length of 1·69 m., and a median length of 1·58 m., corresponding to foetal ages of 7·3 and 7·1 months. Of these 15 foetuses, 12 are between 1 m. and 3 m. in length; the largest at 4·4 m. is equivalent to a foetal age of 10 months, and the two smallest measuring 31 cm. and 76 cm. represent ages of 2·3 months and 4 months respectively. If these three foetuses are excluded then the mean length, 1·66 m., corresponds to a foetal age of 6·95 months, which is probably a better estimate.

The foetuses of lactating females are conceived at a post-partum ovulation, which on average follows closely on the mean calving date at the end of May (p. 403). The lactating females are very near weaning time and allowing about 7 months for the length of the lactation period (to account for the mean foetal age) suggests weaning at the end of December. Mackintosh and Wheeler (1929, pp. 431–7) estimated that the average length of the calf at weaning is probably about 12 m. in the

southern hemisphere fin whale. This estimate was based on an apparent increase in the rate of growth of the baleen plates at weaning, and on the sizes of the largest suckling calves and the smallest independent calves. There is no additional information to give us cause to modify this estimate, although it should be noted that Chittleborough (1958) found no such increase in the growth of baleen in the humpback whale. By plotting the lengths of small fin whales against the time of capture Mackintosh and Wheeler were able to extend their average curve of foetal growth to the lactation period, and found that it attained the level of 12 m. in the first week in December. In the same way they estimated that in the blue whale weaning occurs at an average length of 16 m., which in this species also is attained in December. These authors, therefore, assumed that weaning occurs on average in December, and they pointed out that in each of these species there is a regular influx to South Georgia waters, mainly from January onwards, of small whales, many of which have probably just recently been weaned.

A short paper by Ash (1956) also suggests that weaning occurs on average in December. He expressed the increase in fatness of fin whales by plotting the blubber ratio (average blubber thickness in cm./length of whale in feet) against time. The rate of fattening is fairly constant during the 10-week period covered by the data. Males and non-pregnant females are represented by curves which are almost identical; the curve for pregnant females is well above the curve for non-pregnant females, but is nearly parallel to it, and lactating females are seen to be very lean. The average blubber ratio of the five lactating females given by Ash is 0·279. If we assume for the reasons given above that lactating females are very near to weaning, then this figure is probably very close to the average blubber ratio for non-pregnant females when they first enter the antarctic population (because the non-pregnant group is largely, if not entirely, composed of post-lactation females). When the fatness curve for non-pregnant females is extrapolated backwards in time to a value of 0·279, this is found to correspond to the third week of December. This evidence again suggests December as the average month of weaning.

It will also be remembered that the cumulative curve of ovulations which is held to correspond to the change from lactation to the 'resting' phase reaches the 50% level in December (p. 442).

These several estimates all suggest December as the average month of weaning for the southern hemisphere fin whale. However, when we examine the incidence of lactating females on the whaling grounds, we find that rather small numbers of lactating females figure in the catches for the early part of the season, and are at a maximum towards the end of the season. Thus, at South Georgia, between 1925 and 1931, out of 459 females examined closely, 68 or 14·8% were found to contain apparently normal milk in the mammary glands, but when the monthly proportion of lactating females is examined there are found to be about 5% of mature females in October and November, rising to 44% in March (Text-fig. 50). If weaning occurs on average in December, then most lactating females should be taken in the early part of the season, and by March very few unweaned calves should be left. The fact that the bulk of lactating females in the catches are taken late in the season strongly suggests that in the earlier months lactating females do not enter the whaling grounds in representative numbers, but in fact wean their calves before entering colder waters.

Mackintosh and Wheeler (1929) also commented on the fact that the behaviour of lactating females as a class differs from that of non-lactating females. They also suggest that for part of the nursing period the lactating females are segregated from the main herds, so that not all lactating females appear on the whaling grounds. These authors suggest that lactating females are slower on migration than non-lactating females, and this is borne out by Chittleborough's observations on humpback whales (1953, p. 222). Mackintosh and Wheeler (1929) point out that the killing of females accompanied by a calf is prohibited in the Falkland Islands Dependencies; according to the whalers young calves are

rarely seen in the Dependencies, though relatively common off the South African coasts (p. 433). They also believe that in some cases 'the calf is weaned on the small and rather scarce krill' in South African waters 'and remains in the northerly regions for the first summer' (p. 437).

It is not at all improbable that fin whale calves should be weaned in regions which are not very rich in plankton. Thus, we can be certain that humpback whale calves are almost invariably weaned at the end of a northward migration, in waters relatively poor in plankton (Chittleborough, 1958). The minke whale provides a better parallel with the fin whale. Lactating female minke whales are not found in the Arctic, although they are found in Lofoten waters in small numbers, and Jonsgård (1951) suggested that most are weaned before they immigrate to Norwegian waters from lower latitudes.

It is suggested that in the fin whale the calf is weaned on average in December, and that in the majority of cases weaning occurs north of the antarctic whaling grounds, if not north of the Antarctic
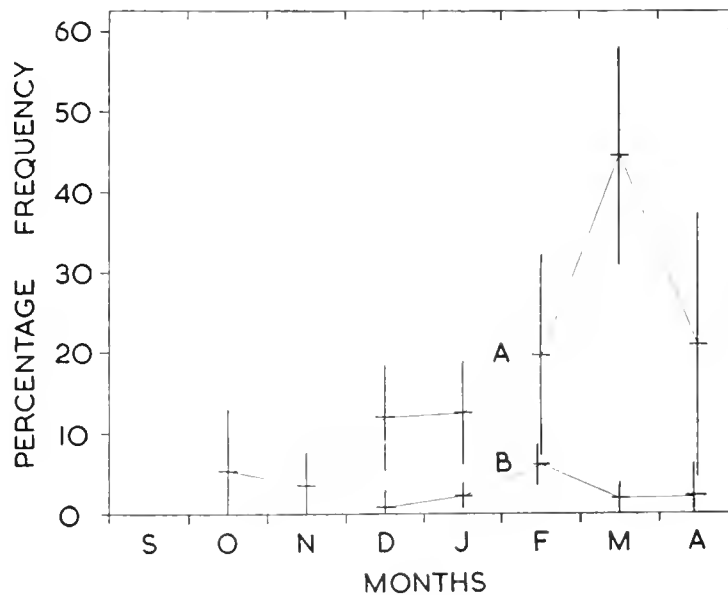
Text-fig. 50. Monthly percentage frequency (± 2 s.e.) of lactating females in the South Georgia catches (A), and the pelagic catches (B) of mature females.

Convergence. It is clear that (even if we allow that lactating females are under-represented in the catches owing to the prohibition on their capture), lactating females are not present on the whaling grounds in representative numbers in the early part of the season. This hypothesis explains why no very early post-ovulation stages in the development of the corpus luteum have been recovered in the Antarctic (p. 443), because if weaning and the post-lactation ovulation usually occur to the north of the whaling grounds, then the very early post-ovulation stages might well be unrepresented or very under-represented on the whaling grounds.

Some lactating females are, however, taken on the whaling grounds, although the evidence presented above suggests that in a large proportion of these the secretion of milk has actually ceased. It may well be that some of the others have also weaned their calves very recently, but that the process of milk secretion has not yet ceased. In this connexion it may be thought to be significant that, in explaining infractions of paragraph 3 of the Schedule to the International Whaling Convention, 1946 (which prohibits the taking of calves or females accompanied by calves), the gunners almost invariably state that no calf was seen. They are heavily penalized for taking lactating whales, but their denials have some support from the evidence given here.

A further point, which should now be discussed, concerns the difference in the incidence of lactating

females in the catches at South Georgia and on the pelagic whaling grounds. The South Georgia figures are based on the biological investigations made during the period 1925–31, and the pelagic figures are from 1939–54 (see Table 25, 'Percentage lactating'). Both samples relate to times and places at which the taking of females accompanied by calves was prohibited. The pelagic sample relates to the 5 months December–April, and the overall proportion of mature females found to be lactating is $3 \cdot 3 \pm 1 \cdot 08 \%$; during these 5 months at South Georgia the proportion lactating was $18 \cdot 9 \pm 4 \cdot 3 \%$. While it is possible that the enforcement of this prohibition was less rigorous at South Georgia in 1925–31 than in British pelagic expeditions from 1939 onwards, it seems possible that such a great difference in the incidence of lactating females in the catches reflects a real difference in the proportion of lactating females in these two populations. If true it would mean that lactating females appear in South Georgia waters in relatively greater numbers than on the pelagic whaling grounds further south.

So far we have expressed the occurrence of lactating females in the catches as a percentage of the total mature females. This is open to the criticism that lactating females are protected to a degree which may well vary with time and place. Text-fig. 50 at first gives the impression that the peak influx of lactating females is later in South Georgia waters than on the pelagic whaling grounds, but this is misleading. It is possible to obtain a much more accurate impression of the seasonal and numerical incidence of lactating females on these two whaling grounds, by applying the percentage figures for lactating females to figures of the total catches of mature females, and thus to obtain estimates of the numbers of lactating females in the catches in different months. The method is similar to that employed when examining the numbers of recent ovulations in antarctic waters (p. 440). The same figures are used for the percentage immature and the source of the data on percentage lactating is given above.

The basic figures used for the catches are for the period 1927–35 for South Georgia (as before) and 1945–47 for the pelagic catches. Data on the latter period are used because they include catches made in December and April. The results are presented in Table 25 and Text-fig. 51, and are to be regarded as approximations for demonstration purposes rather than as precise values. Thus the validity of the early and late catches cannot be checked but should not affect the main conclusions.

Table 25. *Estimated monthly frequencies of lactating females in the catches at South Georgia and on the pelagic whaling grounds*

	South Georgia, eight seasons 1927–35					Pelagic, two seasons, 1945–47				
Month	Catch	Percentage immature	No. mature	Percentage lactating	No. lactating	Catch	Percentage immature	No. mature	Percentage lactating	No. lactating
September	195	(20·0)	156	0·0	0	—	—	—	—	—
October	1348	24·1	1013	5·4	55	—	—	—	—	—
November	1930	15·2	1637	3·6	59	28	15·2	24	—	0
December	2919	18·6	2376	11·8	280	2129	18·6	1733	0·93	16
January	3714	30·7	2574	12·5	322	5861	30·7	4062	2·3	93
February	2136	44·5	1185	19·6	232	6274	44·5	3482	6·0	209
March	879	46·0	475	44·4	211	5284	46·0	2853	1·9	54
April	208	33·3	139	20·8	29	995	33·3	664	2·1	14

In Text-fig. 51 a curve has been drawn which shows the expected monthly incidence of weaning. This curve is the same shape as the curve of calving frequencies (Text-fig. 31), but is displaced in time by about seven months, so that the mean value occurs in December (as estimated above), and the mode is, therefore, at the end of November. Differential growth between birth and weaning should affect the shape of this curve, though not the mode and mean, but it has not been possible to allow for this. The estimated numbers of lactating females in the catches are shown in the same figure for comparison. It will be seen that peak numbers of lactating females were taken in South Georgia

waters in January, and entered the pelagic catches in peak numbers in February. The ascending limb of the pelagic curve actually appears to be about one to two months later than the ascending part of the curve for South Georgia. In drawing this figure the scale, on which the estimated numbers of lactating females have been plotted, has been so arranged that the descending limb of these curves is in advance of the descending limb of the upper curve (which shows the approximate expected frequency of weaning), by about 2 weeks to a month. This is in order to allow for the fact that lactating females taken in antarctic waters are on average estimated to be only 2–4 weeks in advance of weaning. The high value for March in the South Georgia curve reflects the high percentage frequency of
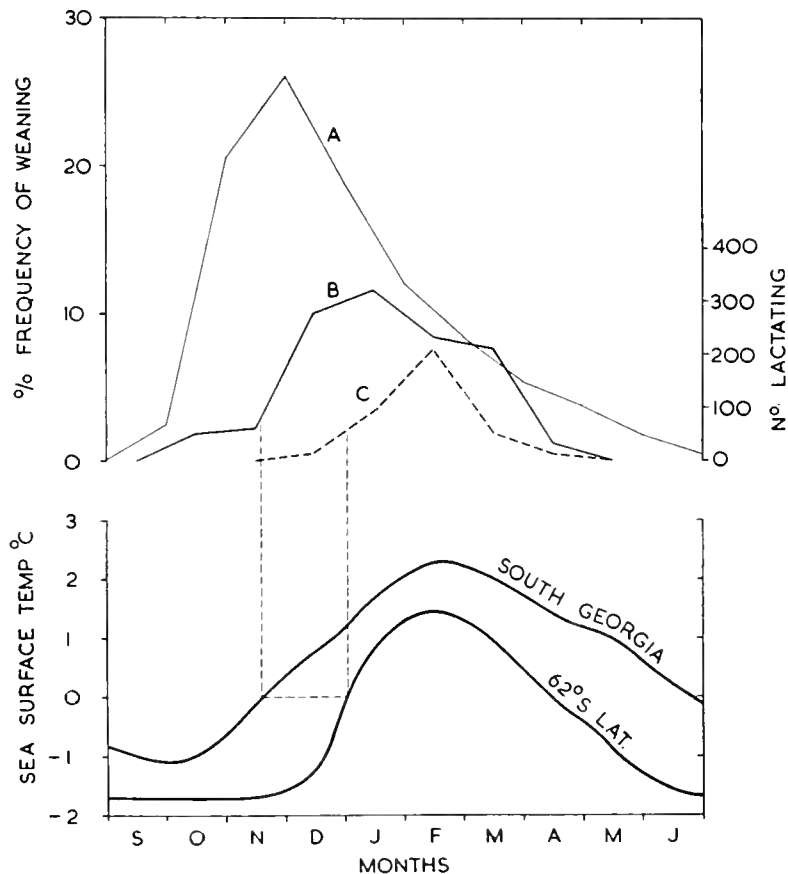
Text-fig. 51. Above: A, estimated frequency of weaning; B, monthly incidence of lactating females in South Georgia catches, and C, in pelagic catches. Below: average monthly sea surface temperatures in South Georgia waters and on the pelagic whaling grounds.

lactating females in the sample for this month (Text-fig. 50); it may well be too high. Even so the slope of the descending limb of the South Georgia curve is fairly close to that of the expected curve.

In explanation of these results, it is suggested that the southward migration of females with suckling calves is dependent on, and limited by, seasonal changes in the temperature of the sea. In latitudes from 56° S. to 66° S. the average sea surface temperature is at a maximum in February (Mackintosh, 1946, fig. 11), when it is 1–2° C. higher than in December or earlier. The average surface temperature for March is also much higher than the December value and somewhat higher than the January surface temperature. Also, the summer rise in the surface temperatures appears not to begin until early January in higher latitudes (64°–66° S.) owing to the presence of sea ice.

In Text-fig. 51 the average monthly sea surface temperatures for South Georgia and the pelagic whaling grounds are plotted for comparison with the curves showing the relative frequency of

occurrence of lactating females in the catches. The temperature curve for South Georgia has been constructed from information given by Mackintosh (1946); the average latitude of the pelagic whaling grounds is assumed to be about 62° S. (see Mackintosh, 1942, fig. 2), and the monthly sea surface temperatures for this latitude are taken from Mackintosh (1946, fig. 11).

Comparison of these sea temperature curves with the curves showing the relative monthly frequencies of lactating females in the catches strongly suggests that the movements of females with suckling calves are closely dependent on environmental temperatures. It appears that the influx of lactating females to the whaling grounds may begin when sea surface temperatures rise above about 0° C., as suggested by the broken vertical lines in Text-fig. 51. This apparently occurs about 5–6 weeks earlier in South Georgia waters than on the pelagic whaling grounds. The figures suggest that over 50% of females enter South Georgia waters after they have weaned their calves, mostly before January, and that probably over 80% wean their calves before they reach the pelagic whaling grounds further south. It was concluded above, that the majority of those lactating females which do penetrate to the whaling grounds later in the season are either very near to the time of weaning, are in process of weaning, or have just weaned the calf.

It is not possible to demonstrate a significant difference in the percentages of lactating females in the pelagic sample at different latitudes, because of the variation in the position of the isotherms in different sectors of the Antarctic. Thus, south of the Atlantic Ocean in January the 0° C. isotherm lies at about 58° S., but south of the Indian Ocean this isotherm is at about 65° S. in January. If the material is subdivided into sectors then the samples are rather too small for statistical analysis to yield significant results.

The conclusions reached in this section are of some importance in connexion with the occurrence of the post-lactation ovulation, because if for the majority of females weaning of the calf and ovulation occur north of the whaling grounds, then the chances of finding very early post-ovulatory stages in the development of the corpus luteum are greatly reduced (see p. 443). They are also important in relation to the supposed danger to the stock of killing lactating females. If the majority of lactating females do not enter the whaling grounds until the calf is weaned, and if those which do are very close to the time of weaning, then the effect on the stock of killing lactating females will not be so drastic as was previously thought.

THE SEXUAL CYCLE AND ITS RELATION TO THE MIGRATORY CYCLE

In an earlier paper, on foetal growth in whales, it was suggested that the explanation of the conspicuous differences in the gestation periods and curves of foetal growth of baleen and toothed whales, was to be found in the discontinuous feeding and the migratory cycle of baleen whales (Laws, 1959a, pp. 304–5).

In a preceding section of this paper (p. 421) it was also shown that the sexual cycle of newly mature females was rather closely related to the migratory cycle, and a possible causative and regulatory factor was suggested. The further evidence which has now been presented shows that a similar correlation is found in multiparous females. This may now be discussed in detail.

The main pairing season for multiparous females is found to extend from April to July, as compared with the period May–September for primiparous females, and the median dates of conception are respectively 8 June and 21 July. Another point of difference is that the frequency curve of multiparous conceptions is skewed, with a long 'tail' from July to December, whereas the primiparous curve is more symmetrical.

If we accept the hypothesis that the sexual cycle in the fin whale is regulated by the change in day lengths related to and caused by the long migrations between low and high latitudes (p. 423), the

advancement of the pairing season in multiparous females is clearly related to the fact that the northward migration of mature females is earlier than that of immature females. Thus, there is an increasing proportion of immature females in the catches towards the later part of the antarctic whaling season, which suggests that immature females migrate into, and move out of, antarctic waters later in the season than mature females. Only 13°₀ of multiparous conceptions are estimated to occur earlier than the beginning of May and this figure is almost certainly too high, because the method of estimation takes no account of variations in the rate of foetal growth. This has the effect of extending the estimated period of conceptions. Thus, in calculating the frequency of conceptions, a faster growing foetus would appear to have been conceived earlier than one which grew more slowly, whereas in fact both might have been conceived at the same time.

According to Text-fig. 42 (p. 423) the earliest period in which whales migrating northwards should experience increasing day lengths is late April–May, and this is in very close agreement with the estimated frequency of conceptions. The latest month during which fin whales can migrate northwards, and yet be subjected to increasing day lengths, is seen to be September, although few if any animals migrate northwards at this time. From July to November or December, animals remaining in one latitude zone in the southern hemisphere will experience increasing day lengths (Text-fig. 42); this extends over most of the period covered by the 'tail' of multiparous conceptions. It is interesting that in the apparently non-migratory female sperm whale pairing occurs in spring (Matthews, 1938; Clarke, 1956), that is at a season of increasing photo-period.

It is not, however, necessary to show that all conceptions follow a period of increasing day lengths, because it has been shown that a post-partum ovulation is a regular feature of the sexual cycle. The factors governing this post-partum ovulation are uncertain, but it is likely that interoceptive factors relating to the end of pregnancy, the regression of the corpus luteum of pregnancy, and loss of the placenta are responsible. In this event conceptions occurring before May could represent a successful post-partum ovulation, for a calf conceived in May would on average be born $11\frac{1}{4}$ months later in April, so that the mother could experience a post-partum heat and mate again in April. In this connexion it will be remembered that the average age of females which conceive in April is apparently very much higher than in later months.

It seems likely that the 'tail' of the pairing curve of multiparous females is largely caused by such post-partum conceptions, and it is perhaps significant that in the closely related blue whale the frequency curve of conceptions obtained from foetal length records is not skewed in this way (Laws and Purves, 1956, fig. 11). In the blue whale post-partum conceptions are not a regular feature of the sexual cycle (p. 429).

We may conclude that the pairing season of multiparous females is closely related to, and perhaps regulated by the increasing day lengths associated with the northward migration from antarctic waters to subtropical and tropical waters. For multiparous females in general, age does not influence the time at which ovulation and conception occur, although the oldest females show a strong tendency to mate early in the season. No convincing explanation of this anomaly suggests itself. It may be relevant that in these older females linear growth is very slow, or has ceased, so that they may not need to remain on the feeding grounds for as long as younger, faster-growing females and can migrate north somewhat earlier.

Detailed examination of the size distribution of corpora albicantia in females in the different phases of the sexual cycle provides strong evidence that the majority of, if not all, adult females experience a post-partum ovulation. It has been shown, however, that a substantial proportion of primiparous females do not experience a post-partum ovulation. The evidence discussed above does not allow a precise estimate of the proportion of females in which the post-partum ovulation initiates another

pregnancy. Some 18% of lactating females in the present material are found to be simultaneously pregnant, but the variance of this percentage is large (S.E. $= 4 \cdot 34$) which means that the true proportion probably lies between 9 and 27%. It may be argued that if a post-partum ovulation is of regular occurrence, then more females should be simultaneously lactating and pregnant. It is, however, quite likely that females are relatively infertile at the post-partum cycle, as compared with the ovulation at the end of the 'resting' period which initiates pregnancy in the majority of females. It is well known that a number of animals, including man, are less fertile during lactation. Similarly, interoceptive factors may govern the initiation of an oestrous cycle after stillbirths and possibly after abortions.

Perhaps the most unexpected result of the present investigation is the evidence for an end-of-lactation or post-lactation oestrous cycle in the fin whale. This is of regular occurrence in the humpback whale, but in this species it occurs in low latitudes. In the fin whale the lactation period is shorter, and a post-lactation ovulation occurs during the migration to the antarctic feeding grounds and is associated with increasing photo-periods. Females taken in antarctic waters with an active corpus luteum of ovulation in the ovaries, denoting a recent ovulation, show a very low incidence of diatom infection, suggesting that they have only recently moved into antarctic waters.

It has been suggested that the southward movement of females with calves is in general restricted to regions where the sea surface temperature is above $0°$ C. Weaning of the calf occurs on average in December, but probably owing to the unfavourable environmental conditions less than half of the lactating females in that sector enter South Georgia waters, and probably less than one-fifth enter the pelagic whaling grounds further south, over a month later. The majority of females, therefore, experience the post-lactation oestrous cycle before attaining the latitude of the pelagic whaling grounds (on average about $61-62°$S.). Almost all lactating females which are present in antarctic waters are very near to the time of weaning, are weaning, or have recently weaned the calf. Many of the lactating females passing through South Georgia waters probably experience a post-lactation oestrus while migrating from the latitude of South Georgia to the pelagic whaling grounds further south.

The few lactating females which penetrate to high latitudes late in the whaling season probably enter oestrus at the end of lactation, but the earliest stages in the development of the corpus luteum which have been accurately noted in antarctic waters, were estimated to be about one week post-ovulation. As only ten such corpora lutea of ovulation have been noted since the recent investigations began, it is not surprising that no very early stages in the development of the corpus luteum have been recorded as yet. In the earlier records some corpora lutea are noted as 'very young', but it is not known whether any of the very earliest stages after the rupture of the follicle and early development of the corpus luteum have been observed. On rare occasions mating has been observed in antarctic waters.

The temporal distribution of these post-lactation ovulations has been investigated, and it is found that very few if any occur before September, that mid-December is the average date, and that no recent corpora lutea are found after March.

It is significant that at the same time as this post-lactation oestrous cycle, pregnant females also experience an ovarian cycle, following a southward movement to antarctic waters. In pregnant females there is a cycle of follicular activity which is at a maximum (expressed as maximum follicle size, and as numbers over 3 cm. in diameter), in December, or November/December. The follicles increase in size, but maturation is suppressed owing to the presence of the corpus luteum of pregnancy. The timing of this cycle is again in close agreement with the hypothesis that pro-oestrus is initiated during a period of increasing day lengths related to the southward migration.

The post-lactation oestrous cycle initiates a pregnancy only very infrequently (in an estimated 5% of

cases). This is probably because there is a single restricted sexual season in the male fin whale. Evidence given above shows that the male sexual season extends in the main from April to July, and is reflected by the data on the frequency of pairing. It agrees with the hypothesis put forward to explain the factors regulating the female cycle. Almost invariably the seminiferous tubules of males are still regressing on arrival in antarctic waters, but full anoestrus is attained soon after arrival.

It is not immediately clear why the male should not experience a sexual season during or following the southern migration as do the females, but there is an important difference between the sexes which may go a long way towards explaining this. The female fin whale is monoestrous and produces ova at infrequent intervals, but in the males it is probable that, as in some other animals, production of sperm is continuous over a period of several months. If we assume a 'refractory period' just after the sexual season (as in fact occurs in female dioestrous cycles), then increasing day lengths would not initiate a further sexual season if they occurred during this 'refractory period'.

Such a refractory period has been shown to characterize the testis cycle of seasonally breeding male birds (Marshall, 1950, 1951). It is defined as 'that period of the avian testis cycle when the tubules are in a state of post-spermatogenetic lipoidal metamorphosis and before the newly regenerated Leydig cells of the interstitium have become sufficiently lipoidal and mature to respond to neuro-hormonal influences initiated by natural factors in the environment'.

This seems to be the most likely explanation, but it is also possible that the testes of male fin whales, stimulated by increasing day lengths on migration, undergo a short recrudescence of activity. If this were so, then it might be expected that more females would become pregnant following the post-lactation ovulation. In juvenile birds, the testis tubules have not produced spermatozoa, and the lipoid Leydig cells are still developing and receptive to stimuli; it is possible that some pubertal male fin whales are similarly receptive to day-length changes during the southern migration, as are pubertal females. In this case some pubertal females might be expected to mate successfully with pubertal males at this time. The disadvantage of such matings is clear; it would mean that larger numbers of calves would be born at a time when the females must seek out food in the colder southern waters. If it is disadvantageous for several-months old unweaned calves to enter antarctic waters then it is clearly very disadvantageous for births to occur in antarctic or sub-antarctic waters.

Marshall (1942) has reviewed the evidence bearing on the role of exteroceptive factors in sexual periodicity. He concludes that in all species of mammals there is an internal sexual rhythm 'which is presumably dependent upon an endocrine cycle but that this is usually, though not always, adjusted to external seasonal change. That the recurrence of the sexual periods is not due entirely to endocrine factors is shown especially clearly by those individuals which belong to species or breeds that ordinarily have only one sexual season annually, yet can be induced to have two seasons by transferring them across the equator from one hemisphere to the other.'

The evidence which has been presented strongly suggests that the ovulatory cycles of fin whales are monoestrous cycles. This conclusion is strongly supported by the evidence as to the limited variation in the rate of accumulation of corpora albicantia presented earlier. Further support for this view will be demonstrated below, when the average annual rate of ovulation, estimated from just such a seasonally monoestrous cycle as has now been described, is found to be in very close agreement with the independent estimate of the average annual rate of ovulation given earlier in this paper (p. 385), and with the rates of ovulation suggested by comparison with other methods of age-determination.

Variation of fertility with age

It has been shown that the female fin whale experiences a seasonally monoestrous sexual cycle. If this is true then variations in the rate of production of ova will be mainly related to the incidence of multiple ovulations, or to the percentage of females ovulating at each ovulatory period, rather than to variations in the number of dioestrous cycles in each ovulatory period.

Multiple ovulations

The varying incidence of multiple ovulations with age in the present material is shown in Table 26. For different numbers of corpora albicantia are shown the numbers of females with more than one corpus luteum in the ovaries. The incidence of multiple ovulations appears to increase with increasing numbers of corpora albicantia (and therefore with increasing age), but there is a significant difference only between the first two groups. It seems probable that there is a real increase in the occurrence of multiple ovulations, because Kimura (1957, fig. 10) shows, for a much larger sample, that the frequency of dizygotic twins similarly increases with age from about 0·1% (at 1–5 corpora) to 6·25% (at 30–35 corpora). The average incidence of multiple ovulations in the present material is 2·16±0·82%. So far we have not considered the variations in actual numbers of ovulations in cases of multiple ovulation. In different cases of multiple ovulations the number of corpora lutea produced varies from 2 to 13 (in the present material). There are 22 females with 2 corpora lutea, 3 with 3 corpora lutea, 1 with 4 corpora lutea and 1 with 13 corpora lutea.

Table 26. *Variation in incidence of multiple ovulations with age*
(number of corpora albicantia)

No. of corpora albicantia	Total ovaries with corpora lutea	Multiple ovulations	Percentage multiple ovulations	2 S.E.
0–4	490	1	0·20	0·40
5–9	281	7	2·49	1·86
10–14	178	5	2·81	2·47
15–19	128	6	4·69	3·74
20–24	76	5	6·58	5·70
25–29	49	—	—	—
30–34	29	1		
35–39	15	1		
40–44	3	1	6·00	6·72
45–49	2	—		
50–54	1	—		
Total	1252	27	2·16	0·82

Table 27. *Details of multiple ovulation in which* 13 *ova were shed and* 5 *foetuses developed*

C.L. no.	Ovary I Weight (lb.)	Ovary I Diameter (cm.)	Ovary I Cavity diameter (cm.)	C.L. no.	Ovary II Weight (lb.)	Ovary II Diameter (cm.)	Ovary II Cavity diameter (cm.)
1	$1\frac{3}{4}$	14·5	—	1	$\frac{1}{2}$	13·0	8·0
2	$\frac{3}{4}$	12·0	6·5	2	$\frac{3}{4}$	10·0	—
3	$\frac{5}{8}$	10·5	—	3	$\frac{1}{4}$	9·0	3·3
4	$\frac{5}{8}$	10·0	6·5	4	$\frac{1}{4}$	7·0	4·5
5	$\frac{3}{8}$	9·5	4·5	5	$\frac{1}{4}$	7·0	4·5
6	$\frac{3}{8}$	9·0	—	—	—	—	—
7	$\frac{3}{8}$	7·5	5·5	—	—	—	—
8	$\frac{1}{4}$	7·5	2·5	—	—	—	—

The appearance of the corpora lutea in the case where there were four simultaneous ovulations is illustrated in Text-fig. 10 *a*. The female which had 13 corpora lutea in the ovaries was examined by Dr R. H. Clarke on 25 February 1948 in 61° 14′ S., 87° 25′ E., and measured 78·5 ft. in length. This female carried 5 male foetuses of lengths 2·03, 2·26, 2·28, 2·54, and 2·67 m., the first of which was necrotic, the others healthy. There were 16 corpora albicantia in the ovaries and details of the 13 corpora lutea are given in Table 27. It will be seen that none of the corpora lutea is of very small size, ranging from 7 to 14·5 cm. in diameter, and all would therefore be expected to leave a permanent record in the ovaries (p. 375).

Making due allowance for these supernumerary corpora lutea it is estimated that on average 1·034 corpora lutea are formed each ovulatory cycle, that is to say the proportion of extra ovulations is 3·4±1·02%. With a smaller sample (part of the present sample) in which the corpora lutea were examined in detail the proportion of accessory corpora lutea was 3·7% (p. 361).

Proportion of females in oestrus or pregnancy

Another aspect of the variation in sexual activity with age can be studied by examining, for successive groups of corpora numbers, the percentage of adult females which show one or more active corpora lutea in the ovaries. The majority of these females will be pregnant, but a small proportion are in a
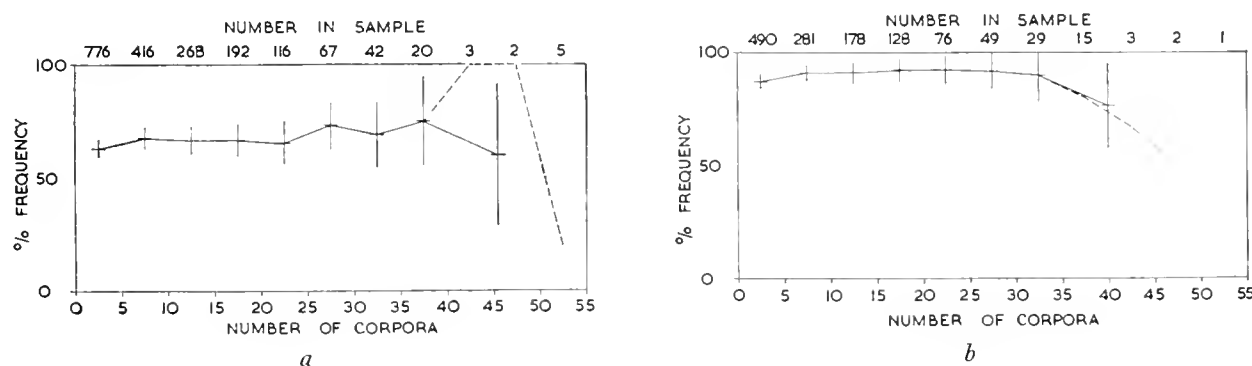
Text-fig. 52. *a*, Percentage of mature females which have an active corpus luteum in the ovaries.
b, Percentage of these corpora lutea which represent pregnancies.

post-oestrus condition following a recent unsuccessful ovulation (p. 437). Owing to differential migration, mortality, etc., the figures obtained will not exactly represent the true proportion of females which are still experiencing oestrous cycles, but will give a picture of the relative variation in activity with age.

The results are shown in Text-fig. 52 *a*, in which data on 1907 mature females examined between 1925 and 1954 are utilized. For successive age groups (expressed as corpora numbers) the percentages of mature females with corpora lutea are shown. The vertical range represents the percentages ±2 S.E., and the results for the last three groups have been combined so as to increase the size of the sample.

Over this range of ages the percentage frequency of pregnancy or post-oestrus stages does not vary significantly, but taking the figures as a whole it would seem that fertility increases very slightly up to an age corresponding to 40–50 corpora (estimated to be about 35–40 years; see pp. 465–66), after which it may decline.

A proportion of these females have ovulated recently without becoming pregnant, and it is, therefore, interesting to see whether the percentage of unsuccessful ovulations varies with age. There are 1252 females in the material which have corpora lutea in the ovaries, and these are again divided into successive age groups according to corpora number. For each age group the proportion known to be pregnant, because a foetus was noted, has been calculated. Some few pregnant females in which the

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foetus was missed may have been included in the non-pregnant group, but this will not greatly affect the results, and in any case the relative incidence of pregnancies is what we are here concerned with. The percentages pregnant ± 2 s.e. are shown in Text-fig. 52 b, and the results for the last four age groups have been combined to increase the size of the sample.

There is again no statistically significant difference in the incidence of successful ovulations, but considering the results as a whole it would appear that the youngest females show a slightly lower fertility, that fertility is at a maximum at ages corresponding to 15–30 corpora (that is about 15–25 years, see p. 466), after which the proportion of successful ovulations appears to decline. This is in agreement with the generalization made by Hammond (1952, p. 656) that the time of submaximal fertility corresponds to the time during which the skeleton is completing its full growth, because as we have seen in the fin whale, ossification of the vertebral epiphyses is completed when 14–15 corpora have accumulated in the ovaries.

There are no data on which to base an accurate estimate of pre-natal mortality, which is another factor in fecundity. This includes all females which conceive, but fail to complete pregnancy successfully, owing to absorption or abortion of the embryo or foetus. In sheep, losses from these causes average 2·4%, but in cows they are higher, averaging 10% (Hammond, 1952, p. 703). It is likely that in whales the average incidence of pre-natal mortality is very low, possibly as low as the average figure quoted above for sheep.

The climacteric which occurs in some mammals, and is perhaps most marked in man, marks the end of active sexual life and is, therefore, the inverse of the developmental process of puberty. It is of rare occurrence in natural populations. Taking into account all the evidence presented above, it is clear that there is no real climacteric in fin whales, at least up to the ages represented in the sample. It is significant that the oldest female (according to the number of corpora which had accumulated in the ovaries) was pregnant. It does, however, seem that there is a slight tendency for fertility to be reduced at ages in excess of about 30–40 years (that is when 35–50 corpora have accumulated, see p. 466).

Variations in fertility with time

Mackintosh (1942, p. 223) referring to blue and fin whales remarked that, 'the percentage of adult females which are pregnant has been increasing in a remarkable degree year by year, as if the actual rate of breeding were becoming faster'. He suggested that this was conceivably a reaction to whaling. Since then additional material has become available.

In order to make use of material collected by non-biologists, so as to keep the available samples as large as possible, all females with an active corpus luteum in the ovaries have been assumed to be pregnant whether or not an embryo or foetus is found. If this procedure were not adopted, then the sample would have to be restricted to females of which the uterus has been carefully searched. This would greatly reduce the size of the sample and would eliminate all samples provided by the whaling companies.

The term 'percentage pregnant' means, therefore, the proportion of adult females in the catches which had an active corpus luteum in the ovaries. The actual 'percentage pregnant' will be lower than this by about 8–10%, because as shown above a proportion of those females which have active corpora lutea in the ovaries are not pregnant, but have recently ovulated.

It should be emphasized that the term 'percentage pregnant' refers to the catches only, and applies to the total population in a relative way. This is due to the fact that a large proportion of lactating females delay the southward migration into antarctic waters (p. 450), and because of this, and also because of the prohibition on the taking of lactating females, this group is under-represented in the catches. This may partly explain the lower values for the South Georgia catches, where more lactating females are taken.

Another factor influencing the apparent percentage pregnant is the mortality rate. Non-pregnant mature females taken in antarctic waters will on average be about a year older than pregnant females, because most females become pregnant at the first ovulation and do not join the non-pregnant group until a year later. Thus, even if lactating females were fully represented in the samples and the actual average pregnancy rate for individual females was 50% (that is, one pregnancy every 2 years), the apparent 'percentage pregnant' of the population as a whole, resulting from an annual adult mortality rate of, say, 20% should be 55·5%. For every 100 pregnant females there would be only 80 non-pregnant, because 20 females die in the intervening year. However, even if the effects of high mortality rates are allowed for, the variation between the values for the apparent 'percentage pregnant' is considerable, and probably represents a real change in fertility. This might be caused by increased fertility at post-partum or post-lactation ovulations, and to a small extent perhaps by reduced pre-natal mortality.

It has been shown above that the youngest females have a lower fertility rate, and that fertility is maximal at about 15–25 years, after which it appears to fall slightly. If the age-composition of the population has changed then this would affect the percentage pregnant, but only to a very slight and possibly not appreciable extent.
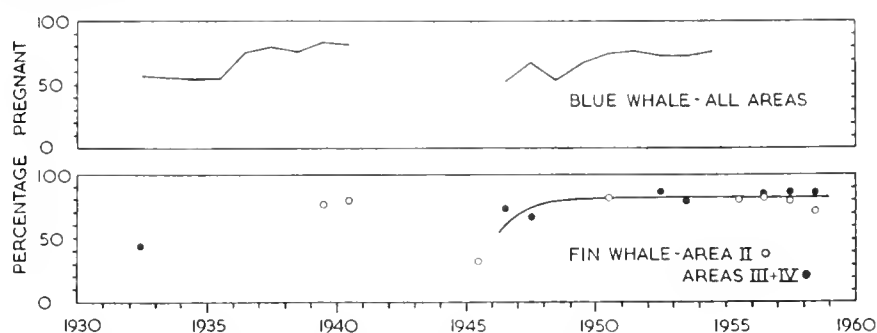
Text-fig. 53. Pregnancy rates of mature females in different seasons and areas.

Table 28. *Variations in the 'pregnancy rate' in the catches of adult females over a number of years*

| | Blue | | | | Fin | | | | | | | Blue | | Fin | | | | | |
| | South Georgia | | Pelagic | | South Georgia | | Area II | | Areas III + IV | | | Pelagic | | Area I | | Area II | | Areas III + IV | |
Season	No.	Per-centage	No.	Per-centage	No.	Per-centage	No.	Per-centage	No.	Per-centage	Season	No.	Per-centage	No.	Per-centage	No.	Per-centage	No.	Per-centage
1925/26	—	—	—	—	72	46	—	—	—	—	1945/46	190	26	—	—	284	32	—	—
1926/27	30	40	—	—	18	56	—	—	—	—	1946/47	479	54	—	—	—	—	66	74
1927/28	—	—	—	—	12	42	—	—	—	—	1947/48	377	68	—	—	—	—	180	68
1928/29	27	41	—	—	74	69	—	—	—	—	1948/49	347	54	—	—	—	—	—	—
1929/30	9	55	—	—	188	69	—	—	—	—	1949/50	239	68	—	—	—	—	—	—
1930/31	25	76	—	—	70	76	—	—	—	—	1950/51	278	75	—	—	80	83	—	—
1931/32	—	—	—	—	—	—	—	—	—	—	1951/52	142	77	—	—	—	—	—	—
1932/33	—	—	184	57	—	—	—	—	25	44	1952/53	134	73	—	—	—	—	61	87
1933/34	—	—	—	—	—	—	—	—	—	—	1953/54	121	73	—	—	—	—	165	80
1934/35	—	—	563	55	—	—	—	—	—	—	1954/55	68	77	—	—	—	—	—	—
1935/36	—	—	407	55	—	—	—	—	—	—	1955/56	—	—	130	69	185	81	—	—
1936/37	—	—	342	76	—	—	—	—	—	—	1956/57	—	—	163	79	294	82	118	84
1937/38	—	—	401	80	—	—	—	—	—	—	1957/58	—	—	108	71	333	79	174	86
1938/39	—	—	506	76	—	—	—	—	—	—	1958/59	—	—	—	—	184	72	363	86
1939/40	—	—	75	84	—	—	222	77	—	—									
1940/41	—	—	39	82	—	—	164	80	—	—									

With these reservations in mind the variations from year to year in the 'percentage pregnant' may be briefly discussed. In Table 28 the full results are shown, and in Text-fig. 53 some of these values are plotted.

The pelagic values for blue whales are combined for all areas, because individual areas show a similar pattern. This indicates an apparent increase in fertility in pre-war years levelling-out at about

80% pregnant. The great reduction in the intensity of whaling during the war years is apparently correlated with a fall in the percentage pregnant to the original low level of the early 1930's. Then, in post-war years, there was a similar increase in fertility up to the 1950/51 season, though it seems that the maximum fertility is lower than in pre-war years. Sampling difficulties may be responsible for this change, because pregnant females are more abundant in the catches early in the season (see above) and the later season for blue whales in recent years would be expected to result in a potentially lower 'percentage pregnant'. The catches of blue whales have declined greatly in post-war years and samples after 1954/55 have been too small to use for this purpose.

The data for fin whales follow a similar pattern and the values for area II and areas III and IV have been plotted separately in Text-fig. 53. Areas III and IV have a similar history of exploitation, beginning long after area II (Text-fig. 54).

The 'pregnancy rate' for the South Georgia fin whale catches rose from about 50% in 1925/26 to 70% or more at the beginning of the 1930's. At this time the annual catches of both fin and blue whales in area II were increasing (Text-fig. 54) (geographically South Georgia is within area II). The pregnancy rate for area II fin whales had risen to about 80% by 1940/41, after some years of high catches in this area (Text-fig. 54), but in 1945/46 after the greatly reduced catches of the war years
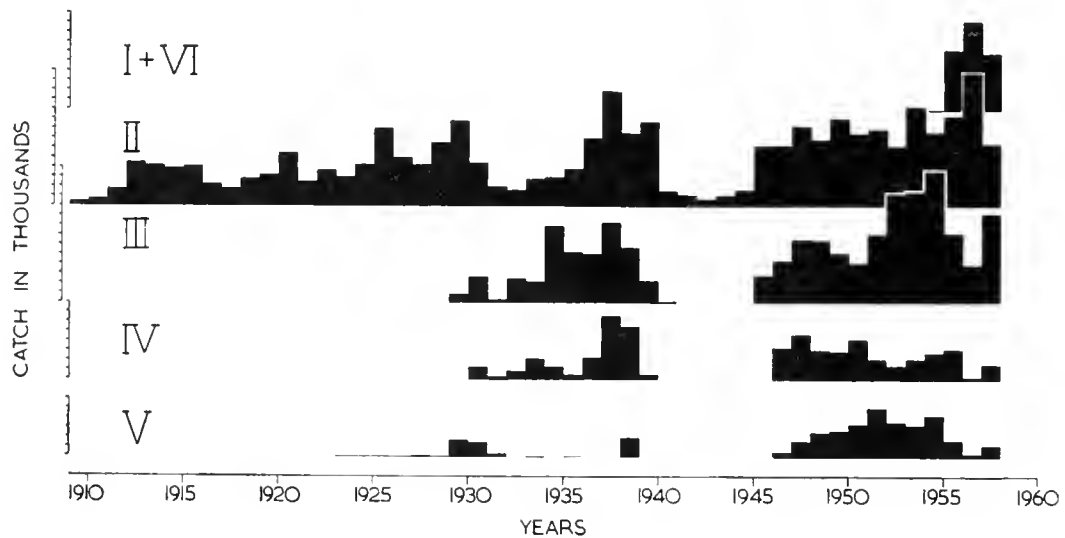
Text-fig. 54. Antarctic catches of fin whales from 1909/10 to 1957/58 according to the whaling areas.

had fallen to 32%. This season was rather an abnormal one and the sample may have been less representative of the stock than in later seasons, but bearing in mind the additional evidence from blue whales, it does seem reasonable to conclude that the real pregnancy rate was low. By 1950/51, after several seasons of sustained heavy exploitation (Text-fig. 54), the 'percentage pregnant' was above 80%. This would appear to be the maximal response of which the fin whale was capable, for in later seasons (1955/56–1958/59) even after larger catches the percentage pregnant was stable at about 80%. The apparent decrease in the pregnancy rate in 1958/59 is disturbing, but may not be real, and it is too early to assess its full significance. Owing to differential sampling as mentioned above, a 'pregnancy rate' of 80% is probably equivalent to a real pregnancy rate of about 60%.

Similarly in areas III and IV the 'pregnancy rate' appears to have stabilized in post-war years at rather more than 80%. A very small sample from area III in 1932/33 suggests a very much lower pregnancy rate, but little confidence can be attached to this figure.

In area I the 'percentage pregnant' was round about 70–80% from 1955–58 when very large catches were being made in this area. Area I was a sanctuary up to 1955/56, so that according to the hypothesis that fertility is lower in natural conditions and rises with increasing fishing mortality, the 'percentage

pregnant' might have been expected to be low in the season 1955/56. There is, however, some evidence from whale marking of interchange of whales between this region and area II, so that the area I whales were probably not a completely unexploited stock before whaling operations began in this area.

What is the most likely mechanism causing such changes in the pregnancy rate? Lack (1954) has surveyed the factors which operate to limit the numbers of mammals. He suggests four density-dependent factors that might be important; food shortage, disease, predation, and, as a secondary factor dependent on food, behaviour. It seems probable that the availability of food is the primary factor limiting the numbers of baleen whales under natural conditions, though man, as a predator, has now largely taken over this role. Food-supply limits numbers by its effect on mortality rates (by starvation); also in several species of mammals, and especially in deer, the birth-rate has been found to vary with the food-supply (Cowan, 1950; Severinghaus, 1951; Morton and Cheatum, 1946; Cheatum and Severinghaus, 1950). The food-supply is density-dependent and so is the birth-rate. It is suggested that the observed rise in the pregnancy rate of fin and blue whales associated with increased exploitation by man is a response to decreased population density acting through the food-supply. It is a limited response which in the fin and blue whales evidently produced its maximum effect by the early 1950's and has since been fairly stable.

It is hoped that a fuller discussion of this apparent relation between fertility and intensity of whaling can be given in a later paper. For the present it is sufficient to show that the bulk of the present material comes from samples collected when the fertility was probably maximal. For periods when the 'percentage pregnant' was appreciably lower than 70–80% (that is, the samples for 1924–28, 1932/33, and 1945/46), the sexual cycle may well have been slightly different from that which has been described above. In particular the percentage of post-partum conceptions may have been lower. This suggestion receives some support from the South Georgia data, because in the period 1924–28 the proportion of lactating females pregnant was very much lower than in 1928–31 (Table 19). See also pp. 430, 437.

If there was a real difference in the sexual cycle for periods when the catches of whales were less, then the annual rate of ovulation may have been slightly different at these times. The difference would not, however, be sufficient to have an appreciable effect on age-determination by means of corpora lutea and corpora albicantia, which is discussed in the following section.

AGE-DETERMINATION BY MEANS OF THE OVARIAN CORPORA

The Rate of Accumulation of Corpora Albicantia

It has been shown above that with negligible exceptions the corpora albicantia in fin whale ovaries, which represent previous ovulations or pregnancies, persist throughout life in a form which is readily visible to macroscopic examination. This persistence on a macroscopic scale is related to the large initial size of the whale corpus luteum, in conjunction with the fact that the corpus luteum usually regresses to a constant fraction of its initial size. The mean diameter of fully regressed corpora albicantia is 2·01 cm. and very few shrink to less than 1 cm. in diameter.

By using a slicing machine to cut 5-mm. thick slices of the ovaries, the number of corpora in each pair of ovaries can be determined with precision, and the errors in counting are small. Earlier samples of ovaries were sliced by hand and although the errors will inevitably be greater the results from this period are unlikely to be much in error, probably not more than ± 5–10%. The numbers of corpora in the ovaries will give us an estimate of the relative age of the female, and if it is possible to determine the average rate of accumulation of corpora, then actual ages may be estimated with a degree of confidence which depends on the variation in the age at puberty and the variability in the average

rate of accumulation. We are now in a position to give an estimate of the average annual rate of accumulation of corpora, and to compare ages determined in this way with ages determined by other independent methods.

Types of corpora albicantia

Three age groups of corpora albicantia have been identified on the basis of gross anatomical appearance, and confirmed by histological examination (p. 366). The mean diameters of these groups in order of increasing age are 4·01 cm., 2·94 cm., and 2·01 cm. These three groups represent stages of regression, and in the ovaries there are on average about 1·54 of the youngest corpora albicantia and 3·22 of the next age group. The number in the oldest group is cumulative, and bears a direct relation to the total number of corpora in the ovaries. That is to say, the first two groups represent stages of regression, while the third group represents the accumulation of fully regressed corpora albicantia which increase in numbers with age.

If the first two groups represent successive stages of regression, their relative frequency of occurrence should represent the relative length of time taken for each stage of regression. It is found that the ratio of 'young' to 'medium' corpora albicantia is almost exactly 1:2 and it appears that together they occupy about three years. The 'young' corpora albicantia, therefore, represent about one year's accumulation, and 'medium' corpora two years. The average annual rate of accumulation of corpora, therefore, appears to be about 1·5–1·6, but a correction (explained on p. 380) is necessary because the process of regression lasts longer in older animals, so that there are more 'young' and 'medium' corpora in the higher corpora groups, that is at higher ages. This suggests that 1·4–1·5 is a more accurate value for the annual increment of corpora.[1] It is found that newly mature females ovulate on average about 1·42 times before becoming pregnant.

The sexual cycle

Evidence has been presented in this paper which strongly suggests that the female fin whale has a seasonally monoestrous type of sexual cycle. It has been shown that in the majority of females there are three ovulatory periods, two of which (a post-partum oestrus and a post-resting oestrus) usually occur in low latitudes in the southern winter, during or after a northward migration; and the other (a post-lactation oestrus), usually occurs in higher latitudes in the southern summer, during or after a southward migration. With the present data it is not possible to show conclusively that these ovulatory periods are invariably monoestrous, but the material available strongly suggests that this is so. The evidence for newly mature females is perhaps the most conclusive. Even if female fin whales are not invariably monoestrous there is certainly a very strong tendency towards the monoestrous condition, similar perhaps to that which has been demonstrated, for example, in certain species of Equidae and Bovidae (Eckstein and Zuckerman, 1956, pp. 238, 245).

In this connexion it is of interest that Chittleborough (1954) has shown just such a strong tendency to monoestrus in the humpback whale during the breeding season. Thus, he finds that the mean number of ovulations for a female humpback whale during its ovulatory period (in Australian waters) is only slightly over one. It is possible that the monoestrous condition in the fin whale is more apparent than real, and that there is in fact a polyoestrous cycle in which the first ovulation is almost invariably successful. However, in an ovulatory period, such as the post-lactation oestrus of the fin whale, when males are out of breeding condition, the polyoestrous cycles should not be suppressed. The evidence on this point, both in females at puberty and in adult females, is strongly in favour of monoestrous cycles in fin whales at each of the three ovulatory periods. This evidence precludes more than a slight tendency towards polyoestry.

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[1] From the evidence of the corpora albicantia the possibility that the rate is only 0·7–0·75 cannot be excluded (see p. 385).

Given a seasonally monoestrous sexual cycle it is possible to estimate the average annual rate of ovulation. It should be made clear that this evidence is completely independent of the other estimate of the rate of ovulation given in this paper. Thus, ignoring for the moment post-partum and post-lactation conceptions and assuming that all females experience a post-partum and post-lactation oestrus, there would on average be three ovulations in two years, or 1·5 a year. The effect of post-partum conceptions and post-lactation conceptions will be to alter this estimate as follows.

The incidence of the post-partum ovulation and the percentage of conceptions resulting from it are the points on which there is most uncertainty. Calculations have, therefore, been made for six different alternatives, in which it is assumed that the incidence of post-partum ovulations is either 100 or 80%, and three alternatives are assumed for the proportion of successful post-partum ovulations, namely 9, 18, or 27%. The post-resting ovulation is assumed to be 100% successful, and the post-lactation ovulation is assumed to be only 5% successful. An allowance of 3% is made in respect of multiple ovulations. Evidence has been given earlier supporting a high incidence of post-partum ovulations (pp. 429–36); the alternative proportions of post-partum conceptions are based on the average incidence plus or minus 2 s.e. (p. 430); reasons have been given for assuming a low incidence of post-lactation conceptions (p. 443), and the frequency of multiple ovulations has been discussed.

The calculations are presented in Table 29, and because in calculating the average annual rate the starting-point in the 2-year cycle is important, three hypothetical 2-year periods are covered.

In the first case the 2-year cycle is assumed to commence in late pregnancy, so that the first ovulation occurs at the post-partum oestrus. Then, in the first column it is assumed that all females ovulate shortly after parturition and that 9% conceive at this time. Then 91% will enter anoestrus until the post-lactation ovulation, at which 5% of them will conceive, so that 87% of the original numbers are left to ovulate again at the end of the resting period. It is assumed that these become pregnant and do not ovulate again for nearly a year. An allowance must be made for those females which become pregnant at the first post-partum ovulation in this cycle. They will ovulate again at the end of this pregnancy, and 91% of them (because 9% are assumed to become pregnant again), will ovulate once more at the end of lactation. These figures should include all the ovulations in this 2-year period. When allowance is made for multiple ovulations by adding 3%, the mean value for this case is 1·518 ovulations per year.

The other columns are worked out in the same way, the results varying with the basic assumptions.

In the next set of calculations (Table 29 B, column 1), the 2-year sexual cycle is assumed to commence just before the winter post-resting ovulation. All females are assumed to ovulate at this stage of the cycle, becoming pregnant for nearly a year when, as in the case set out in the first column, all experience a post-partum ovulation, and 9% conceive at this ovulation. The remaining 91% ovulate again at the end of lactation, and 5% of them are assumed to become pregnant again. The 2-year period ends before another ovulatory period is due. A correction is again made to allow for multiple ovulations, and the mean value for this set of premises is 1·499.

In the third group of calculations (Table 29 C, column 1) the sexual cycle is assumed to begin just before the post-lactation ovulation, when all ovulate with 5% conceiving. Thus, 95% are left to ovulate at the post-resting ovulation, when they become pregnant again and ovulate post-partum just before this arbitrary 2-year period ends. The other 5% which became pregnant at the first post-lactation oestrus should experience a post-partum ovulation at the end of the first year when 9% of them (that is, about 0·45% of the original sample) should again become pregnant. This leaves 4·55% to ovulate again at the end of lactation, when they are all assumed to become pregnant (because this ovulation should occur in winter, in low latitudes, when males in breeding condition are present). After an adjustment for the occurrence of multiple ovulations, the mean value is estimated to be 1·543.

Table 29. *Calculation of average annual rate of ovulation. Three 2-year periods are considered, beginning with a post-partum oestrus* (A), *a post-resting oestrus* (B), *and a post-lactation oestrus* (C). *See text for explanation*

Ovulatory periods	100% post-partum ovulation			80% post-partum ovulation		
	9% P.L.	18% P.L.	27% P.L.	9% P.L.	18% P.L.	27% P.L
A. *Beginning with post-partum oestrus*						
1. Winter (post-partum)	1·000	1·000	1·000	0·800	0·800	0·800
2. Summer (post-lactation) 5% success	0·910	0·820	0·730	0·910	0·820	0·730
3. Winter (post-resting) 100% success	0·865	0·779	0·694	0·865	0·779	0·694
4. Winter (post-partum)	0·090	0·180	0·270	0·072	0·144	0·216
5. Summer (post-lactation)	0·082	0·148	0·197	0·082	0·147	0·197
	2·947	2·927	2·891	2·729	2·690	2·637
Multiple ovulations (3%)	0·088	0·088	0·087	0·082	0·081	0·079
	3·035	3·015	2·978	2·811	2·771	2·716
Annual rate of ovulation	1·518	1·508	1·489	1·406	1·386	1·358
B. *Beginning with post-resting oestrus*						
1. Winter (post-resting) 100% success	1·000	1·000	1·000	1·000	1·000	1·000
2. Winter (post-partum)	1·000	1·000	1·000	0·800	0·800	0·800
3. Summer (post-lactation) 5% success	0·910	0·820	0·730	0·910	0·820	0·730
	2·910	2·820	2·730	2·710	2·620	2·530
Multiple ovulations (3%)	0·087	0·085	0·082	0·081	0·079	0·076
	2·997	2·905	2·812	2·791	2·699	2·606
Annual rate of ovulation	1·499	1·453	1·406	1·396	1·350	1·303
C. *Beginning with post-lactation oestrus*						
1. Summer (post-lactation) 5% success	1·000	1·000	1·000	1·000	1·000	1·000
2. Winter (post-resting) 100% success	0·950	0·950	0·950	0·950	0·950	0·950
3. Summer (post-partum)	0·050	0·050	0·050	0·040	0·040	0·040
4. Winter (post-lactation) 100% success	0·046	0·041	0·037	0·046	0·041	0·037
5. Winter (post-partum)	0·950	0·950	0·950	0·760	0·760	0·760
	2·996	2·991	2·987	2·796	2·791	2·787
Multiple ovulations (3%)	0·090	0·090	0·090	0·084	0·084	0·084
	3·086	0·081	3·077	2·880	2·875	2·871
Annual rate of ovulation	1·543	1·541	1·539	1·440	1·438	1·436
Average of A, B *and* C						
A	1·518	1·508	1·489	1·406	1·386	1·358
B	1·499	1·453	1·406	1·396	1·350	1·303
C	1·543	1·541	1·539	1·440	1·438	1·436
Total	4·560	4·502	4·434	4·242	4·174	4·097
Average	1·520	1·501	1·478	1·414	1·391	1·366

This procedure has been followed for the other assumed rates of post-partum ovulations and post-partum conceptions, and the resulting annual values are averaged. The six mean values finally obtained vary from 1·366 to 1·520, which means that if the assumptions cover almost all the possible range of variation in the incidence of ovulations, the annual rate is between about 1·35 and 1·55. Some of these assumptions are considered to be more likely than others; it is thought to be probable that the incidence of post-partum ovulations lies between 80% and 100% (probably nearer to 80%), and that the proportion conceiving at this ovulation is about 18%. Taking the average of columns 2 and 5 in the final line of Table 29 gives a figure which meets these conditions and suggests an average annual rate of

ovulation of 1·446. Assuming the incidence of post-partum ovulations to be nearer to 80%, we may adopt a figure of about 1·43 ovulations per year. Even if the incidence of post-partum ovulations is as low as 60%, which is improbable, the average annual increment (for 18% pregnant/lactating) is 1·282.

If the fin whale is not strictly monoestrous, but only shows a strong tendency to this condition, then the average annual rate of ovulation will be slightly higher than this estimate. An average of 1·1 ovulations per ovulatory period (excluding multiple ovulations) would raise the estimate from 1·43 to 1·57, but in the absence of supporting evidence this possibility has not been allowed for in adopting an estimate of 1·43.

There are now two independent estimates based on the evidence presented in the present paper, which are in fairly close agreement, namely about 1·4–1·5 (p. 385) and about 1·43. Allowing for possible causes of variation or sources of error it is considered that the average annual rate of ovulation in the southern hemisphere fin whale is 1·43±0·1. In calculating ages from the numbers of corpora albicantia in the ovaries the annual rate of accumulation is taken to be 1·43 corpora albicantia. In general estimates of relative individual ages, post-puberty, are likely to be accurate to within ±7% (namely ±1·4 corpora, that is, 1 year, in 14 years)[1].

Recovered whale marks

A long-term programme of whale-marking was initiated in 1934–35 by 'Discovery' Investigations, and continued after the war by the National Institute of Oceanography and other interested bodies in Norway, Japan, Russia, Australia, and New Zealand, with the support of the International Whaling Commission and the Whaling Companies (Brown, 1954; Chittleborough and Godfrey, 1957; Clarke and Brown, 1957; Dawbin, 1956a; Mackintosh, 1942; Rayner, 1940).

One of the objects of this marking programme was to provide a check on methods of age-determination. Unfortunately, however, there are difficulties which are peculiar to whale research. It is not possible to capture whales, mark them and then release them as in marking fish, seals, and other animals. Whale-marking is effected by firing a numbered metal tube into the dorsal muscle of the free-swimming animal—a costly operation. One consequence of this is that it has not so far been possible to confine marking to one particular known age-class (e.g. the calves), nor is it possible to determine the age or size of individual whales at the time of marking. In any case measurements of body length are very variable, even within a single age-class, and estimates of size in the water are usually inaccurate.

Up to the season 1958/59 about 5000 fin whales had been marked in antarctic waters and 373 marked whales had been recovered up to 1958/59, one of which had a minimum age (from marking to recapture) of 24 years.

Unfortunately only 10 of these recoveries were also accompanied by material (the ovaries) enabling us to make an attempt to check this method of age-determination. The reason for this very low figure (only 4% of the females from which marks were recovered), is that usually the processing of the carcass is well advanced before the mark is found. A fair proportion of the marks are not found until the cookers are cleaned some hours, or days, after processing.

[1] A rate of ovulation of 0·7–0·75, suggested as a possible alternative (p. 385) appears to be incompatible with the evidence of the sexual cycle. Such a low rate is only possible if the cycle is markedly different from that described here. Thus, it would be necessary to accept much lower ovulation rates at the post-partum and post-lactation periods (of the order of only 10–30 %) in order to bring the ovulation rate into line with a value of 0·7–0·75. It is possible that the incidence of post-partum ovulations is lower than has been assumed; the crucial evidence for this relates to the relative sizes and rates of regression of corpora albicantia (pp. 430–4, and especially p. 433). The assumption of a high incidence of post-lactation ovulations is thought to be well-founded (see pp. 436–44). The evidence considered as a whole favours the higher rate of ovulation.

We have then, 10 whales (all except one marked between 1934 and 1937) for which a minimum age is known and for which data on the number of corpora in the ovaries are available. Particulars of these whales are given in Table 30. What is it possible to say about these data?

For these individuals the mean period between marking and recovery is 13·8 years (ranging from 2 to 24 years) and the mean number of corpora is 15·7 (ranging from 3 to 40). If fin whales are marked on average at about the time of puberty (when corpora begin to accumulate) then these data suggest the mean increment of corpora is likely to be about 1·14 per year. If, on the other hand, they tend to be younger or older than this stage when marked, then the average annual increment of corpora is likely to be respectively more or less than 1·14, with the reservations imposed by the small size of the sample. (It is, however, interesting that the sample is equally divided between whales less than, or more than 15 years from marking to recovery. The 'apparent' annual increment is the same in both groups, namely 1·14.)

Table 30. *Particulars of ten marked female fin whales from which the ovaries have been recovered (see text)*

Mark no.	Date marked	Date recorded	Years	Number of C.L. + C.A.	Length of whale (ft.)	Condition
696	11 Dec. 1934	26 Feb. 1941	6·21	8	76	Non-pregnant
1199						
1203	18 Jan. 1935	2 Mar. 1954	19·12	11	76	Pregnant, foetus 2·35 m.
1300						
3507	26 Feb. 1935	18 Jan. 1956	20·89	23	70	Pregnant, foetus 4·33 m.
4938	21 Dec. 1935	13 Jan. 1948	12·06	14	73	Pregnant, foetus 2·77 m.
7972	4 Jan. 1937	19 Feb. 1948	11·13	5	69	Pregnant, foetus 3·35 m.
6818	9 Jan. 1937	28 Jan. 1954	17·05	40	75	Pregnant, foetus 3·35 m.
10504	21 Dec. 1937	16 Mar. 1940	2·23	10	71	Pregnant, foetus 3·95 m.
2627	27 Dec. 1934	20 Jan. 1959	24·06	32	69	Pregnant
*6137	22 Mar. 1936	4 Feb. 1958	21·87	11	74	Pregnant, foetus 2·77 m.
12870	7 Nov. 1955	29 Jan. 1959	3·23	3	70	Pregnant or recent ovulation
Total			137·85	157		
Mean			13·8	15·7		
* Total excluding no. 6137			115·98	146		
Mean excluding no. 6137			12·89	16·2		

There is some evidence bearing on the question of whether female fin whales are marked on average before or after puberty. There are 24 female fin whales marked in the pre-war operations which were recovered either in the same season (o-group) or a year later (1-group), for which the lengths at recovery were known (Rayner, 1940). The mean length at marking should be below the mean length (plus 2 S.E. of the mean) of the animals in this sample. It is known that the mean length of southern hemisphere female fin whales at sexual maturity is 65·25±0·32 ft. (p. 407). The mean length of the o-group and 1-group sample is 65·42±2·18 ft. (mean and two standard errors), and this figure is probably a little high. It is well known that length measurements made on floating factories tend to be slightly higher than control measurements made by biologists, and the effect of the minimum length regulations might be to exclude some of the smaller females from the o-group and 1-group recoveries. It has been shown that the average rate of growth at the period corresponding to these lengths is rapid, amounting to some 3 ft. per year (p. 413), which has the effect of minimizing errors in estimating the age at marking. It is, therefore, probable that the mean age of these whales at marking was a little less than the mean age at puberty, say half a year, because the sample includes roughly equal numbers of o-group and 1-group females. The length variation (±2·18 ft.) corresponds to an age variation of

$\pm$0·67 years, assuming that growth is at the rate of just over 3 ft. a year at this part of the growth curve.

It appears then that about 15·7 corpora accumulate in from 12·63 to 13·97 years (13·3$\pm$0·67 years), that is, at a rate of about 1·24 to 1·12 per year. So far it has been assumed that the ten mark recoveries with ovary data are a random sample from the population. This is probable, but the variance for such a small sample is large, and the true mean rate of accumulation may be higher or lower than this figure. There is also another source of error which must be mentioned.

In the confusion of work on the deck of a whale factory ship there is a possibility that ovaries may sometimes be collected by mistake from the wrong whale. It seems likely that this was the case with mark number 6137. The female from which this came was 22 years from marking to recapture, but the ovaries which accompanied this mark contained only one corpus luteum and 10 corpora albicantia. The baleen plates had the appearance of those of a young whale. It seems probable that this was such a case of mistaken identity, because by a remarkable coincidence two marks were recovered that same day, on the same factory ship, by the same man, both from female fin whales of identical lengths. For one (mark no. 12673) the mark is noted as having been 'found in the dorsal muscle'; for the other (mark no. 6137) there is no note of the location of the mark. Now, if a mark was found in the dorsal muscle it is probable that the ovaries would be obtainable as well. It is, therefore, possible that the ovaries were actually from the whale which bore mark no. 12673, which was only 3·22 years from marking to recovery. This would raise the mean annual rate of accumulation calculated in this way to 1·30–1·46 corpora. In view of this uncertainty it will probably be best to ignore the doubtful record and to repeat the calculations for the 9 mark recoveries about which no doubts have been raised. Then it is estimated that in about 12·39$\pm$0·67 years on average some 16·2 corpora have accumulated, that is about 1·24–1·38 per year (or 1·31$\pm$0·07).

Two other females shown in this table (nos. 1199/1203/1300, and no. 7972) are at first sight incompatible with a rate of ovulation of 1·43$\pm$0·1 per year, but it should be emphasized that this is a mean value. Even if ovulations in these two were at the rate of 1·4 a year, then the apparent discrepancies in the mark data can be explained by assuming that these females matured late (at 11 years and 8 years respectively). If the rate of ovulation were lower then puberty could have been attained earlier.

We can have little confidence in this evidence from the recovery of marked females, which is inconclusive (owing to the small size of the sample), but does not necessarily disagree with the estimated average increment of 1·43$\pm$0·1 corpora per year, obtained from studies of the ovaries and the reproductive cycle. This is the best we can do with the limited data. In view of the difficulty of recovering whale marks together with other data, it seems unlikely that a precise confirmation of this method of age-determination for the fin whale (or of any method) will be obtained for many years, (but see footnote p. 470).

AGE-DETERMINATION

For average growth curves or for population studies the corpora counts may be used to determine the post-pubertal age using the estimated figure of 1·43$\pm$0·1 for the average annual rate of accumulation. For animals which have not attained puberty the method cannot of course be used.

The estimated age at puberty averages 5 years (p. 407), varying in individuals at least from 3 to 8 years in a small sample, and the extreme range is probably greater. There will, therefore, be a considerable variation in individual ages estimated in this way, according to whether the female became mature at an early or a late age. A simple calculation shows that this variation alone would result in a variation of $\pm$4 corpora at a given absolute age. This is in reasonably close agreement with the

frequency curves for the number of corpora in baleen group v females, and for the number of corpora at the attainment of physical maturity. Thus, in the curve showing the number of corpora at the attainment of physical maturity (Text-fig. 27), 81 % are in the range ±4 corpora about the mean. As pointed out earlier (p. 392) it is unlikely that all females attain physical maturity at exactly the same age, or even at exactly the same number of years after puberty. The discrepancy between the estimated range of variation in a single year class and the actual range of variation at the attainment of physical maturity is probably largely to be explained in this way. Also, the mean age and the age range at puberty may be slightly greater than our small sample suggests; ear-plug laminations may not always be formed biannually in immature females; and a further fact to be allowed for is the incidence of multiple ovulations (p. 454).

The close agreement between the expected frequency distribution of ovarian corpora, as calculated from the age variation at puberty, and the actual frequency distribution at physical maturity, supports the earlier conclusion (p. 384) that there is very little variation in the annual rate of ovulation and accumulation of corpora. This is further evidence against the conception of a polyoestrous sexual cycle in which, during an ovulatory period, a variable number of ovulations may precede that which initiates pregnancy.

It is considered that the number of corpora in the ovaries of a fin whale female, of any particular age, will probably be within the range of the mean number of corpora expected at that age ±4; this corresponds to an estimated age which will probably vary from the true age by up to ±3 years. In exceptional cases the apparent age may differ from the true age by more than this. For instance, the combined effect of an early puberty and a number of multiple ovulations would be considerable.

For estimating individual ages the number of ovarian corpora excluding corpora atretica (p. 382) and pathological bodies (p. 343), is divided by 1·43, and to the result is added 5 years, to allow for the immature period. For animals taken in the Antarctic half a year is then subtracted. Thus first pregnancy females taken in the Antarctic with an average of 1·43 corpora are on average estimated to be $5\frac{1}{2}$ years old. The result should then give the probable age to ±3 years with about 90% accuracy. For example, a female with 28 corpora in the ovaries is estimated to be 19±3 years old.

In using the counts of ovarian corpora to determine the age for purposes of average growth curves, population studies, etc., this individual variation can safely be ignored, because in a large sample individual variations caused by early or late puberty, multiple ovulations, etc. will counterbalance each other.

Comparison with other methods

The method of age-determination based on the external ridges of the baleen plates which was developed by Ruud (1940 and later papers) has already been referred to (pp. 335–37). Unfortunately this method is limited in application to the younger age groups, and is, therefore, complementary to the method based on the ovaries of mature females. Over the range of ages where the methods overlap, the latest work of Ruud (1958) suggests that the annual rate of accumulation of corpora, according to the ages determined from baleen records, is about 1·6. This is in fairly close agreement with the present estimate (1·43±0·1 corpora per year).

After the present work had begun a new method of age-determination was suggested by Purves (1955). This arose out of studies on the physiology of hearing in Cetacea, in the course of which it was found that the ear-plug in the external auditory meatus of baleen whales is of a laminated structure. The core of the plug consists of a number of concentric laminations which follow the curvature of the so-called 'glove-finger'. Each lamination consists of epidermal elements derived from the zona corneum of the 'glove-finger'. From the presence of imperfectly keratinized epithelium in each

lamination it seemed that the growth of the epidermis is arrested at regular intervals. It was assumed that the period of arrested growth corresponds to the migratory periods (when the physiological demands of active swimming coincide with complete absence of food), so that each lamination represents a growth period of approximately six months. Later Purves and Mountford (1959, p. 137) stated that 'It is very doubtful whether environmental conditions have any direct influence on the time of formation of the laminae of the ear plug in whales, although nutritional conditions may to some extent determine their thickness. Since there is strong evidence [not given by them] that lamina formation is an inherent moulting cycle it is very probable that it takes place whether the whale migrates or not. If the rate of moulting can be established the ear plug would probably be a more accurate age indicator than the fish scale.'

Comparison of ages estimated in this way from the ear-plug with the corresponding baleen plates for a small sample of North Atlantic fin whales (Laws and Purves, 1956), suggested that the hypothesis
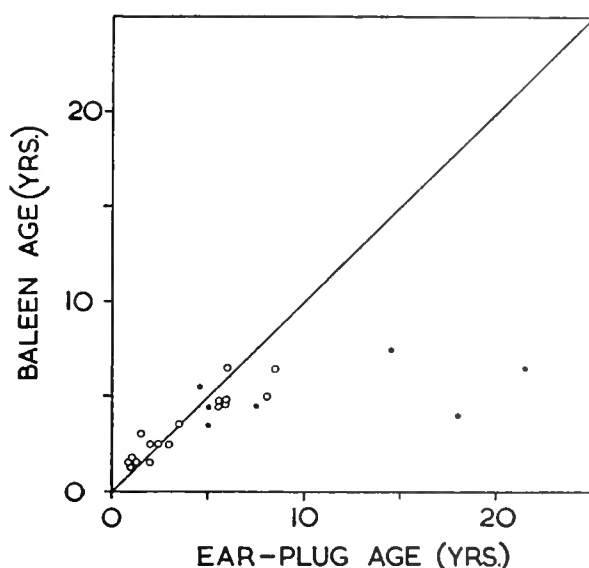
Text-fig. 55. Comparison of the ages of individual fin whales estimated from baleen plates and ear-plugs (white, North Atlantic; black, Antarctic).

of a biannual formation of laminations was correct. This agreement between baleen plates and ear-plugs was partly confirmed with a small additional sample of antarctic fin whale material collected in 1955–56. The ear-plug ages of this sample (estimated on the basis of two laminations per year) are given by Purves and Mountford (1959) to whom the material was made available. Professor J. T. Ruud and Mr Åge Jonsgård (Statens Institutt for Hvalforskning, Oslo) kindly undertook the examination of the baleen plates. In Text-fig. 55 the ear-plug ages are plotted against the ages estimated from the baleen plates. If the age-determinations by these two methods are in exact agreement then the points should fall on the 45° line which is shown. It is apparent that there is fairly close though not exact agreement between these two methods for the first 4–5 years, after which baleen plate ages (owing to wear at the tip of the plates) are supposed to be minimum values. Chittleborough (1959) finds similar agreement between baleen plates and ear-plugs of humpback whales.

Purves (1958) and Purves and Mountford (1959) used the assumption that about 1·4 corpora are accumulated annually in the ovaries of fin whales (Laws, 1956a) to confirm the assumed biannual rate of lamina formation in sexually mature females. Some 14–15 corpora accumulate in the ovaries between puberty and physical maturity, and this period is, therefore, estimated to be 10 years (but see p. 388, where attention is drawn to an error in this work). About 12 laminations were found at

sexual maturity and about 32 at physical maturity, corresponding to an incremental rate of approximately two a year. It was also found that the mean curve of growth in body length gave lengths at the 12th and 32nd laminations which were close to the previously estimated lengths at sexual maturity and physical maturity.

So far the best evidence for the biannual formation of ear-plug laminations, therefore, comes from this check against the ovaries, using the figure of 1·4 for the annual increment of corpora. The nature of the fin-whale sexual cycle, particularly of the female, which was discussed earlier in this paper suggests additional strong circumstantial evidence in favour of a biannual cycle of lamina formation. It also suggests a possible exteroceptive factor responsible for the regular formation of the laminations. Owing to the migratory cycle, most fin whales are usually subjected each year to two periods of increasing day lengths. In the female these are associated with oestrus (incompletely suppressed during pregnancy). In the male it appears that the period of increasing day lengths associated with the spring migration does not initiate a second period of sexual activity, because, it was suggested, of the long period of spermatogenesis which precedes this migration and is followed by a refractory period. This is paralleled by the suppression of oestrus in pregnant females.

One of the most characteristic features of oestrus is the cornification of the vaginal and other epithelia. It seems possible that the growth cycle of the ear-plug is in fact related to the migratory cycle as was initially assumed, not because of arrested growth associated with the expenditure of energy on migration, but because of a biannual hormonal cycle associated with and regulated by varying day lengths. According to this hypothesis there is during each migration a rise in the amounts of circulating oestrogens in both male and female, which results in the formation of a keratinized layer.

This hypothesis explains lamina formation in adults satisfactorily, but little is known of the migrations of immature fin whales and the early laminations are the most difficult to interpret. This interpretation for adults is to some degree independent of the estimated figure for the annual increment of corpora, so that the ear-plug age estimates are at least partly independent of the ovaries.

Purves and Mountford (1959) give the ages, estimated from ear-plugs, of samples of fin whales, and the ovaries of the females in these samples have been examined by the present author. Individual ages have been estimated from the corpora numbers in the way described above (p. 466). In Text-fig. 56 the ages estimated from ear-plugs are plotted against the ages estimated from the ovaries for 111 individuals. The 45° line shown corresponds to an exact agreement between the two methods.

It is expected that, owing to individual errors in the estimates based on corpora numbers (related in the main to the variation in the age at puberty), the majority of the ovarian ages should lie within ±3 years of the regression line representing exact agreement. It is assumed that the ages estimated from the ear-plug laminations are accurate, although some plugs are difficult to read and may give inaccurate results. Also the interpretation of immature laminations is doubtful. Purves and Mountford (1959) estimate the maximum error by this method to be ±2 years. In Text-fig. 57, the variation of ovary ages about the theoretical mean regression line is shown. This curve was constructed by drawing in other oblique lines parallel to the original regression line, displaced laterally at yearly intervals. The total number of points lying within each pair of lines was obtained and plotted to show the frequency distribution about the assumed mean. The results are near to expectation; 72% of the estimated ovarian ages lie within ±3 years, and 82% within ±4 years of the regression line showing an exact correlation, and the extreme range is ±12 years. Only seven values lie outside the range ±6 years and it is probable that the five extreme values represent combined errors of the two methods. The results are in close agreement with the distribution of corpora at physical maturity, shown in Text-fig. 27. It should be noted that there is a group of points in Text-fig. 56, for which the ovarian ages are too high. This is because 5 years is taken as the age at puberty, and some nine of these records

(indicated by a dotted line) are probably from females which attained puberty earlier than 5 years. If it were possible to allow for this the frequency distribution in Text-fig. 57 would be slightly more symmetrical.
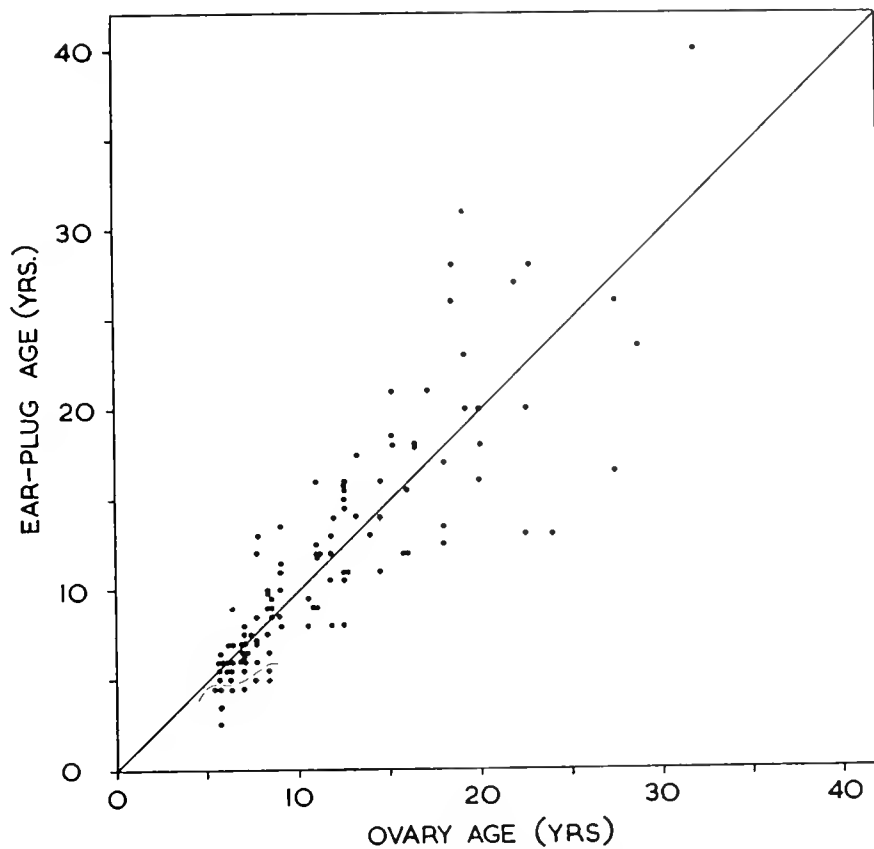
Text-fig. 56. Comparison of the ages of individual female fin whales estimated from ear-plugs and ovaries.
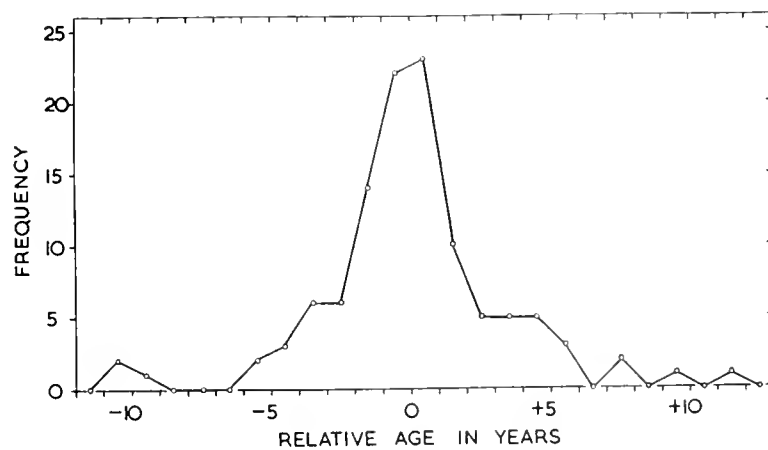
Text-fig. 57. Frequency distribution of ovary ages about the regression line shown in Text-fig. 56.

This brief comparison with other methods of age-determination supports the conclusions about the rate of ovulation and the accumulation of corpora reached in this paper. Ovarian counts may be used with confidence to estimate the ages of mature female fin whales.

Ages determined independently by the three most important methods in use for baleen whales (ovarian corpora, baleen plates, and ear-plugs) are in reasonably close agreement, but all three methods have been criticized on the grounds that it has not yet been possible to check any of them against

animals of known age. If the validity of any one of the methods could be confirmed by reference to known-age animals, then, in view of the agreement between the results obtained separately by the other methods, it could be taken that all three methods are valid for studies of the age-composition of the catches. In the 25 years since effective whale-marking began, only 10 marked fin whales have been recovered together with material enabling age-determinations to be made. It seems unlikely that there will be any great increase in such recoveries in the near future, and for the time being the sample now available is the only independent check on age[1]. The estimated annual increment of corpora and the figure suggested by these marked females are very similar, but owing to the small size of the sample the apparently quite close agreement is not conclusive. There can, however, be no reasonable doubt that the ovaries provide reliable estimates of age, and that the ear-plugs and baleen plates (with some reservations) are also reliable.

One important qualification is called for. The estimated ages are greatly dependent on the method of examination. In this respect the counts of ovarian corpora are perhaps least liable to error. The interpretation of baleen plates is difficult, and the same applies to the ear-plug. In this connexion reference must be made to the recently published papers of Ohsumi, Nishiwaki and Hibiya (1958) and Nishiwaki, Ichihara and Osumi (1958). These authors, by plotting lamination number against corpora number, and assuming two laminations are laid down each year, obtain a figure of 0·8–0·9 for the average annual increment of corpora in northern and southern hemisphere fin whales. Their results differ in this and other respects from Nishiwaki (1957), Purves and Mountford (1959) and the present paper. It seems likely that interpretations of the ear-plug laminations differ (and/or counts of corpora), and a standardization of methods is desirable.

Applications

Survival curves

Having shown that the corpora albicantia persist throughout life and accumulate at a regular rate, it is possible to use corpora counts, made on samples of the antarctic catches since 1925, to investigate the changing age structure.

A full detailed treatment of this subject would be out of place here, but to indicate the possibilities let us take as an example the data for the two seasons 1939/40 and 1940/41, for Antarctic area II (0° to 70° W.). For this period there are corpora counts relating to 389 adult females, 170 from the season 1939/40 and 219 from 1940/41. Brown (1954) has shown that there is little dispersal between the different whaling areas, but suggests that there may be a significant interchange between areas I and II. Virtually no whaling had been carried out in area I, prior to 1955/56 and it may be assumed for present purposes that the whales in area II constitute a stock which is separate from the other areas.

This sample from area II (1939–41) has been chosen because it is fairly large and of the samples available is probably least influenced by changes in the size of the catches. The age composition of post-war samples is affected by the low level of catching between 1940 and 1945. From Text-fig. 54 it would appear that for the effect of fluctuating catches to be minimal the most suitable samples should come from area I in 1955/56, area III before 1934, area IV before 1937, and area V before 1930. If the populations of fin whales in the different areas are distinct and isolated (though not in a genetical sense) such samples might enable estimates of the natural mortality rates of adult females to be made. Unfortunately adequate samples meeting these conditions are not forthcoming.

Three possible methods of constructing survival curves have been examined and although, owing to sampling difficulties none of them is really satisfactory, they can be used to compare the changes in the stocks from year to year in a relative way.

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[1] Since this was written there has in fact been an increase in the number of such recoveries in Japanese factory ships.

First, we could assume that mortality is constant with respect to age, so that the decline in numbers is logarithmic. A regression line is fitted to the logarithms of the corpora albicantia or age frequencies and, if it can be assumed that the age composition of the catch is fully representative of the population being studied, the slope of this line is e^{-zt}, the survival rate, and z is the instantaneous mortality rate, including both fishing mortality and natural mortality. If working in annual age groups then $t = 1$ but with corpora albicantia t is assumed to be 1·43.

This method was used by Purves and Mountford (1959), with reservations, for their fin whale data. The method used by Hylen *et al.* (1955) requires similar assumptions. It seems, however, that in view of the limitations of our samples this method is not applicable and gives a spurious impression of accuracy. Our present knowledge of the relation between the catch and the real population is sufficient to indicate only that confident estimates of absolute mortality rates cannot be given by these methods (nor, so far, by other methods). A detailed discussion of the sampling problem cannot be given here, though a short discussion of some relevant problems will be found in a paper by Laws (1960). However, some of the more important factors which are relevant must be briefly mentioned at this point.

An important problem is related to the segregation of the stocks on the Antarctic whaling-grounds. Laws (1960) has discussed geographical segregation and segregation in time.

The catches show a definite pattern of body size segregation by longitude, when mean lengths are plotted by 10° sectors of longitude, perhaps related to food and oceanographic conditions. This may reflect a geographical segregation by age, which would have important implications for the analysis of age distribution in the catches from different parts of the whaling-grounds.

Fin whales migrate to the antarctic feeding-grounds at different times according to age, sex and reproductive status. The whaling operations, on which we depend for our samples, do not extend over the whole of the summer months when whales are on the feeding-grounds and in recent years the whaling season has become much shorter and generally later. This means that the different age groups in the population are not equally vulnerable to whaling, because they are at risk for different periods. In the fin and blue whales the oldest animals appear on the feeding-grounds first, younger animals next and the youngest last of all. The period when samples are taken may therefore have a profound effect on their age composition. For example, if separate survival curves are constructed for monthly samples taken in November, December, January, February and March the slope is found to be steeper with the progression of the season. Because the older animals tend to arrive on the grounds earlier they may be at risk longer and some of the younger animals arrive after the whaling operations have ceased, so that there may tend to be a bias towards older animals in the age-composition of the catches. An example of this type of selection can be seen in samples from area II in 1939–41 (Text-fig. 58), and from area I in 1955/56 and 1956/57 (Laws, in press).

In exploited stocks of fish it can usually be assumed that recruitment, although varying from year to year, does not change progressively over a number of years in response to exploitation. Although brood strength fluctuations affect the scatter about a curve they do not alter the slope. In whales which bear a single young, recruitment is very closely related to the number of adult females (fluctuating within rather narrow limits) so that in general changes in the size of the stock of adult females will be accompanied by similar changes in the number of recruits. Such changes will affect the slope of the catch curves; the effect of reduced recruitment will be to produce a lower apparent mortality rate.

A further difficulty is that in a long-lived animal changes in overall mortality rates only become gradually apparent as new year classes enter the exploited part of the population. If there is no differential selection of animals in respect of age, above a certain size governed by the minimum length regulations, the relative age-composition of the mature population should change only slowly and the

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effect of varying intensity of whaling should show initially only at the ages when animals enter the catches. It should take many years for these changes to work their way through the age structure of the population, for the catches of fin whales may be drawn from as many as fifty year groups. Marks have been recovered from antarctic fin whales as long as 26 years after marking (the first effective marking was carried out in 1932/33).

Thus even if the catch were a random sample of the stock in the sea important changes could take place in the stock without being detected by the calculation of instantaneous mortality rates derived from a regression line fitted to the catch curve. This method will give only a crude approximation to mortality rates operating over a period of years, and mortality rates derived in this way may be misleading when applied to current situations.

The catch per unit effort gives an index of abundance of the stock. In estimating current mortality rates the most satisfactory treatment would perhaps be to convert the sizes of year classes at two known times to comparable values, by applying effort values so as to obtain density indices for different age groups. Estimates of mortality can then be made from pairs of successive years for different year classes fully recruited to the exploited part of the stock. Unfortunately, the unit of effort in whaling is not stable owing to increasing catcher efficiency (see Laws, in press) and it has not yet been possible to calibrate these changes in effort so that they can be used to estimate mortality rates. This is potentially the most accurate approach, though sampling difficulties and changing recruitment again pose serious problems.

A method which will give us some indication of changing mortality rates is to construct time-specific survival curves by smoothing the frequency distribution of corpora numbers (Table 31) more or less heavily, according to the size of the sample. The resulting curve is converted by a graphical method to an age frequency distribution by finding the values corresponding to $1\cdot43$, $2\cdot86$, $4\cdot29$ corpora up to $52\cdot91$ corpora (equivalent to post-pubertal ages of $\frac{1}{2}$ year, $1\frac{1}{2}$ years, $2\frac{1}{2}$ years and $37\frac{1}{2}$ years). An additional 5 years must be allowed for the immature period, making the ages $5\frac{1}{2}$, $6\frac{1}{2}$, $7\frac{1}{2}$ and up to $42\frac{1}{2}$ years (Table 32).

Direct observation of the age structure of juveniles is not possible by this or any other method because of the minimum size limit, which means that early year classes are absent or not fully represented in the catches. An indirect method must, therefore, be used to estimate the recruitment to the population.

The data given in Table 32 show a total of 2681 females. For present purposes it may be presumed that fertility does not change with age (see p. 454). The conception rate is taken to be $1\cdot18$ per 2-year cycle, assuming 18% post-partum ovulations (p. 430), that is $0\cdot59$ per year. No allowance is made for post-lactation conceptions, or for twins, because it is thought that post-natal survival of these groups is low. On this basis 2681 adult females represent 1582 conceptions. The foetal sex ratio was shown to be 52% male: 48% female so these females are estimated to carry 759 female foetuses. Let us allow 10% prenatal mortality to cover foetal deaths from conception to birth and maternal deaths from mid-pregnancy to parturition. This figure is based on an assumed 5% foetal mortality and about 12% maternal deaths, the latter estimated from table 32. (An assumed stable population of 2681 mature females has a recruitment at puberty of 325 or 12%, which should be balanced by a corresponding number of deaths.) Then 683 female calves are expected to be born, the earlier qualifying remarks about sampling being understood to apply. These data indicate that total immature mortality assuming a stable population is $52\cdot4\%$. If the population from which this sample is derived was decreasing then the immature mortality would be higher than this value.

This 'apparent' survival curve is plotted on a logarithmic scale in Text-fig. 58. The logarithmic scale has the advantage that a straight line implies equal rates of survival (or mortality) with respect

to age. The curve is similar to the diagonal type of Pearl and Miner (1955) and Deevey (1947), but it represents both natural and fishing mortality. A prominent bump in the curve from 20 to 35 years suggests some bias towards older females in the sample as might be expected in view of the tendency (mentioned above) for older animals to be over-represented in the samples. This is a further warning

Table 31. *Frequency distribution of corpora, and apparent survivors up to an age corresponding to 55 corpora. Area II, 1939–41.*

No. of corpora	Frequency	Smoothed frequency × 10 (time specific)	Survivors (dynamic)	No. of corpora	Frequency	Smoothed frequency × 10 (time specific)	Survivors (dynamic)
1	39	350	389	29	5	42	50
2	21	310	350	30	3	44	45
3	34	280	329	31	7	42	42
4	20	244	295	32	4	38	35
5	25	236	275	33	2	44	31
6	22	210	250	34	3	36	29
7	17	186	222	35	6	34	26
8	21	168	211	36	3	38	20
9	8	138	190	37	3	40	17
10	16	128	182	38	4	28	14
11	7	100	166	39	4	22	10
12	12	104	159	40	—	16	6
13	7	94	147	41	—	11	6
14	10	72	140	42	—	9	6
15	11	88	130	43	1	7	6
16	6	84	119	44	—	5	5
17	10	78	113	45	—	4	5
18	5	66	103	46	1	3	5
19	7	68	98	47	—	3	4
20	5	52	91	48	—	3	4
21	7	52	86	49	—	2	4
22	2	50	79	50	—	2	4
23	5	52	77	51	—	2	4
24	6	46	72	52	2	2	4
25	6	48	66	53	—	1	2
26	4	44	60	54	2	1	2
27	3	42	56	55	—	1	0
28	3	36	53	Total	389	—	—

Table 32. *Apparent survival data for area II fin whale females prior to 1940*

Age (yr.)	Survivors Time specific	Survivors Dynamic	Age (yr.)	Survivors Time specific	Survivors Dynamic	Age (yr.)	Survivors Time specific	Survivors Dynamic
$5\frac{1}{2}$	325	370	$18\frac{1}{2}$	59	91	$31\frac{1}{2}$	23	11
$6\frac{1}{2}$	280	330	$19\frac{1}{2}$	53	82	$32\frac{1}{2}$	16	6
$7\frac{1}{2}$	245	290	$20\frac{1}{2}$	49	77	$33\frac{1}{2}$	10·5	6
$8\frac{1}{2}$	210	256	$21\frac{1}{2}$	46	70	$34\frac{1}{2}$	7·0	6
$9\frac{1}{2}$	180	225	$22\frac{1}{2}$	44	62	$35\frac{1}{2}$	4·8	5
$10\frac{1}{2}$	142	200	$23\frac{1}{2}$	42	55	$36\frac{1}{2}$	3·6	5
$11\frac{1}{2}$	135	182	$24\frac{1}{2}$	40	51	$37\frac{1}{2}$	3·0	4
$12\frac{1}{2}$	120	162	$25\frac{1}{2}$	39	45	$38\frac{1}{2}$	2·5	4
$13\frac{1}{2}$	105	148	$26\frac{1}{2}$	38·5	38	$39\frac{1}{2}$	2·0	4
$14\frac{1}{2}$	92	137	$27\frac{1}{2}$	38	31	$40\frac{1}{2}$	1·6	4
$15\frac{1}{2}$	83	122	$28\frac{1}{2}$	37	28	$41\frac{1}{2}$	1·4	2
$16\frac{1}{2}$	73	113	$29\frac{1}{2}$	34	21	$42\frac{1}{2}$	1·2	2
$17\frac{1}{2}$	64	100	$30\frac{1}{2}$	30	16	$43\frac{1}{2}$	1·0	0
						Totals	2681	3361

against reading too much into the apparent survival curve and against describing the age structure by a single regression line.

A third method of constructing an apparent survival curve is the dynamic method which assumes that the sample represents the ages at death. In the present case the sample represents deaths due to whaling and does not take into account natural mortality. However, the adult natural mortality rates of fin whales should be very low to counterbalance the low reproductive rate and long life-span and are probably constant over most of the age range. If we accept the fact that sampling difficulties mean that estimates of absolute mortality rates derived from survival curves are unreliable and not contemporary, we can still expect to obtain limited information on changes in the stocks by comparing the shapes of apparent survival curves. While it is true that neither method is really satisfactory this is thought to be preferable to calculating instantaneous mortality rates from the slope of a single
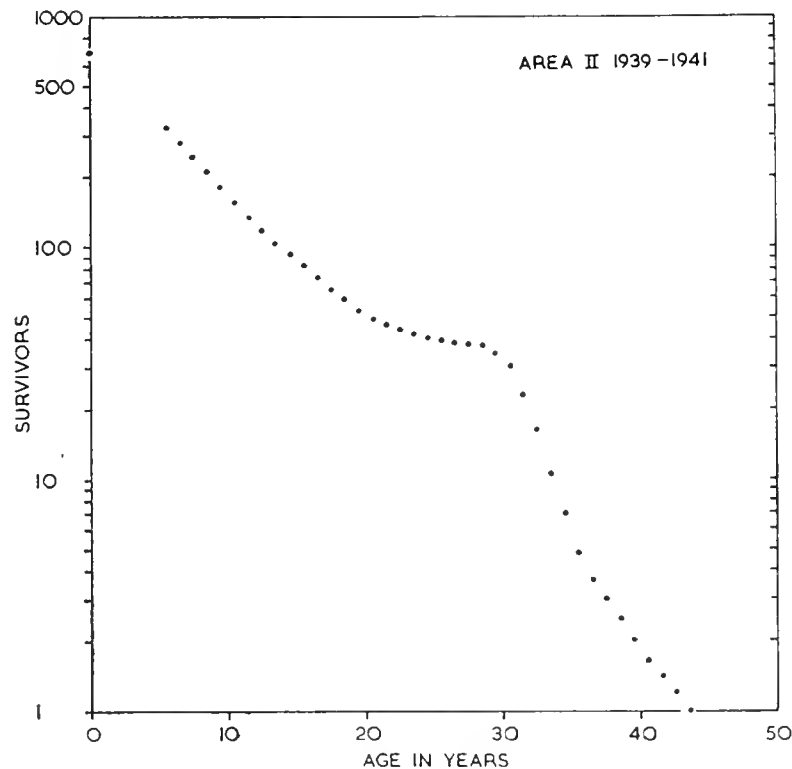
Text-fig. 58. Time specific survival curve for female fin whales. See text for method of construction.

regression line. For this purpose dynamic survival curves appear to be more desirable. Bias towards the catching of older animals (see above) will be shown in the dynamic curves as lower survival rates or higher mortality rates (which is correct) rather than as higher survival or lower mortality as in time specific curves.

Dynamic survival data for the mature females is given in Table 32. These are derived from the counts of corpora albicantia in the following way. There are 389 individuals in the sample and all of these have survived to an age corresponding to one corpus luteum or corpus albicans; there are 39 individuals in the 1-corpus group, from which it is inferred that only 350 survive to the 2-corpora group; 21 individuals in the 2-corpora group are then subtracted to give the number which survive to the 3-corpora group, in this case 329; and so on up to the 55-corpora group when there is no sur-vivor. These data are converted to actual age data as before by finding the values corresponding to 1·43, 2·86, etc. corpora and the result is set out in Table 32 and Text-fig. 59. Recruitment at birth

is calculated as before to be 857 indicating a total immature mortality from birth to 5 years of about 53·3°₀, a very similar result to that given by the time specific method.

This apparent survival curve again approximates to the diagonal type (Text-fig. 59). Mortality appears to be higher in the early segment of the curve and increases again after 25–26 years. Between 9 and 26 years the survival curve plotted on a logarithmic scale is almost exactly linear, that is to say the decline in numbers is exponential. For this segment of the curve the apparent rate is $e^{-0\cdot0973}$ or 90·8%, corresponding to an annual mortality rate of 9·2°₀.

One of the central problems of whale research is to define and distinguish the different populations being sampled; a complementary problem concerns the extent to which the samples from the catches are representative of the actual population in the sea. Until more progress is made in the solution of these problems it would seem that population studies will lack precision.
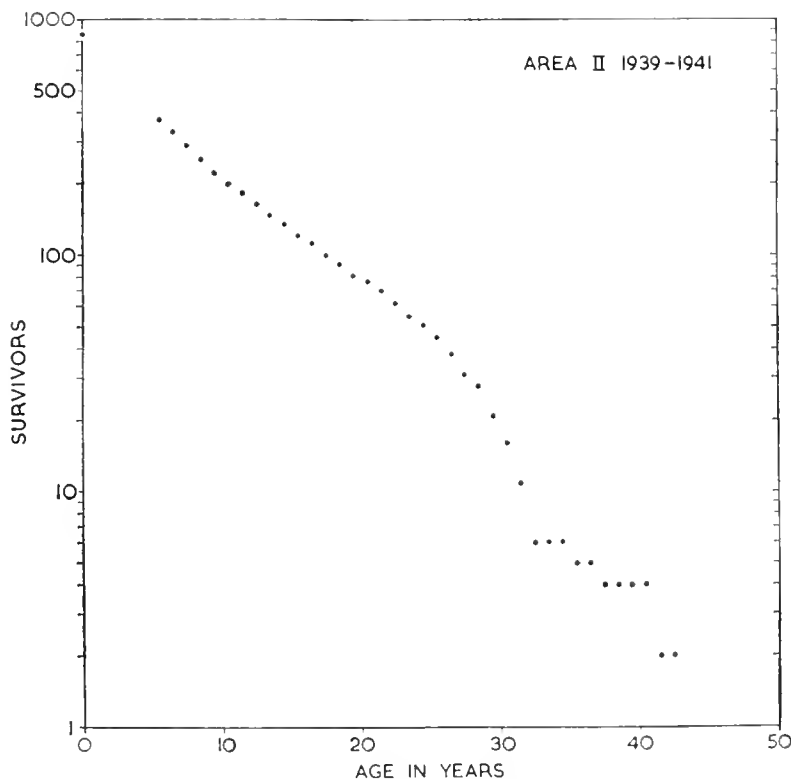
Text-fig. 59. Dynamic survival curve for female fin whales. See text for method of construction.

Growth curves

The relation between length and corpora number for area II females has already been discussed (Table 6, Text-fig. 25). The average length at physical maturity was there taken to be 73 ft., which was the average length of 187 females which had more than 20 corpora in the ovaries. Nishiwaki, Ichihara and Osumi (1958) suggest that after the attainment of physical maturity there is a slight decrease in body length and the present material also suggests this, although the shrinkage is evidently slight and there is no statistical support for it. The relative growth curve in Text-fig. 25 was, therefore, fitted to the average lengths at different corpora numbers so that it attained 73 ft. at 14·3 corpora.

This smoothed curve may be converted to a length-at-age curve in the same way as the age structure of a sample was obtained (p. 466). The lengths corresponding to 1·43, 2·86, 4·29 corpora, etc., are equivalent to post-pubertal ages of about ½ year, 1½ years, 2½ years, etc., and as before an additional 5 years is added to allow for the immature period (Table 33).

In Text-fig. 60 these length-at-age data are plotted. In addition the estimated mean length at puberty (65·25 ft. at 5 years) and the estimated mean length at weaning (39 ft. at 7 months) are shown. The pre-natal growth is known from the previous studies (Laws, 1959 a; and above, Text-fig. 30). Conception is taken to be 0·93 years before birth.

Table 33. *Length-at-age data for female fin whales (see text)*

Age	Stage of life-cycle	Body length (ft.)
0	Birth	20·80
7 months	Weaning	39·00
5 years	Puberty	65·25
5½ years	—	67·80
6½ years	—	69·70
7½ years	—	70·80
8½ years	—	71·60
9½ years	—	72·20
10½ years	—	72·50
11½ years	—	72·70
12½ years	—	72·85
13½ years	—	72·95
14½ years	Physical maturity	73·00
> 15 years	—	73·00

The von Bertalanffy equation (von Bertalanffy, 1938; Beverton and Holt, 1957) has been fitted to the length-at-age data for mature females in area II (Table 33), 5½ years and over, obtained from the smoothed curve showing average lengths at different corpora numbers. This gives a theoretical curve in which $l_t = L_\infty(1 - e^{-k(t-t_0)})$, and a good fit is obtained for values at estimated ages above 5 years. It is shown in Text-fig. 60 as a continuous line for which $L_\infty = 73\cdot0$ ft., $K = 0\cdot450$, and $t_0 = 0\cdot368$. The parameter t is the post-conception age in years. This theoretical curve has been extrapolated backwards to $t = 3\cdot93$, that is equivalent to a post-natal age of 3 years.
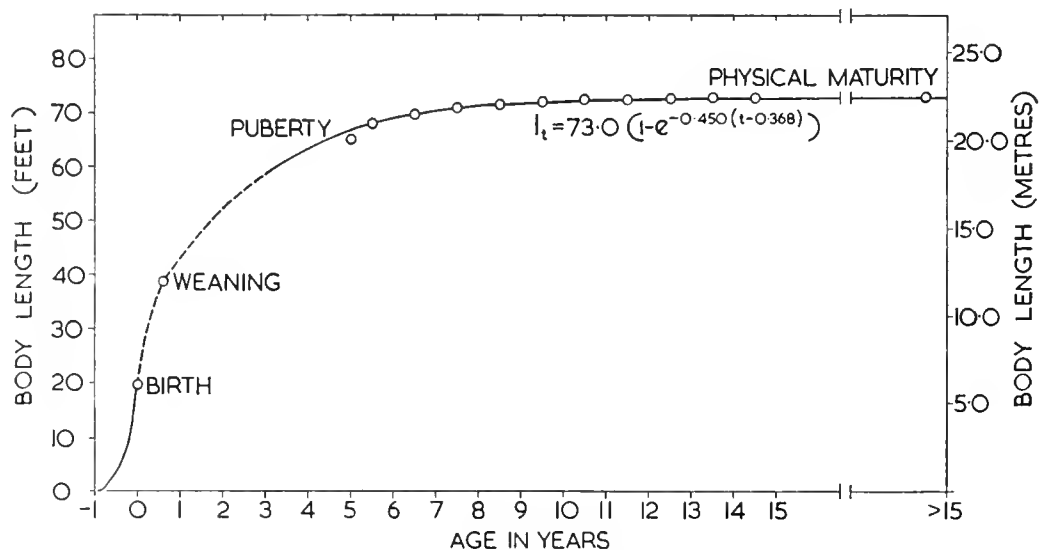
Text-fig. 60. Length-at-age curve for female fin whales, Antarctic area II.

This growth curve has been completed by inserting the foetal growth curve already obtained, with a mean neo-natal length of 20·8 ft. This leaves the segment of the curve from birth to 3 years to be completed, but we have an approximate value for the length at weaning (39 ft.; Mackintosh and Wheeler, 1929), and the age at weaning has been established as about 7 months (p. 445). This has been used to complete the growth curve and agrees quite well with expectation. The equation

$l_t = 73 \cdot 0 \ (1 - e^{-0 \cdot 45(t - 0 \cdot 368)})$ gives values, for the ages corresponding to birth and weaning, of 16·3 and 29·7 ft. respectively. These are quite close to the observed values and the accelerated growth towards the end of gestation and during the lactation period is, as it were, superimposed on the theoretical curve.

The existence of such a close correspondence between the theoretical curve and the observed values makes for additional confidence in the figure of 1·43 for the estimated annual increment of corpora.

There is, however, one discrepancy which will have been noticed in Text-fig. 60. The estimated value for the mean length at puberty (65·25 ft.), which has been inserted at a point corresponding to an age at puberty of 5 years, is not in agreement with the theoretical curve derived from the von Bertalanffy equation (which in fact gives a value of 67·02 ft. at this age). This requires some explanation.

Although growth in body length has here been described by a smooth curve, it almost certainly occurs in a series of steps related to the periods of intensive summer feeding in antarctic waters, and partial winter fasting in low latitudes. This was discussed especially for newly mature females, when it was concluded that there was probably a rapid acceleration of growth associated with the summer feeding period (Text-fig. 38). The values from which the theoretical curve has been calculated are mean lengths for females taken during the same period of the year in antarctic waters when feeding on krill, and are therefore directly comparable. The value for the mean length at puberty was inferred from the length frequency distributions of immature and mature females, and is not, therefore, comparable with the other values. The estimated mean age at puberty obtained by a similar method is 5 years, and therefore represents the time of year when growth is thought to be minimal. This partly explains why the length at puberty calculated in this way is below the theoretical curve. Another reason for this is that the data on length and corpora numbers apply to the area II sample only, whereas the mean length at puberty was calculated from all available data, representing several areas. There is reason to believe that the length at puberty in area II may be slightly higher than the general level in the Antarctic (see also p. 407).

SUMMARY

1. This paper is concerned primarily with female fin whales, *Balaenoptera physalus* (Linn.), and is based on several thousand whales examined in antarctic waters by or on behalf of 'Discovery' Investigations between 1925 and 1949 and on behalf of the National Institute of Oceanography from 1951 onwards.

2. In an introductory section, previous work on the reproductive cycle, migratory cycle, growth and age of baleen whales is briefly reviewed.

The main part of the paper falls into three parts. The first deals mainly with the detailed structure of the ovaries, the evidence for the persistence of corpora albicantia, and the estimated annual rate of accumulation; the second part describes the annual sexual cycle, and provides a further independent estimate of the rate of ovulation; the last section is concerned with age-determination by means of the ovarian corpora, and some examples are given to illustrate the application and value of the method.

3. The mean paired ovary weights of immature, non-pregnant mature and pregnant females are respectively 0·97, 1·97, and 3·14 kg. The increased weight of the ovaries of pregnant females is only partly explained by the development of the corpus luteum. Increased vascularization, and increased follicle size and numbers probably account for the rest. The maximum paired weight of fin whale ovaries was 52 kg., but these were probably in a pathological condition.

4. The morphology and anatomical relations of immature and adult ovaries are briefly described.

5. Primary follicles begin to develop in the last 2–3 months of gestation; they are numerous in the cortex of the ovaries of immature females, but are very sparsely distributed in the cortex in sexually

mature females. In the majority of immature females the largest follicle is less than 1 cm. in diameter, but at the approach of puberty the mean maximum follicle size rises to about 3 cm. or more between June and November.

In mature females the mean maximum follicle size is greatest in the 'recently ovulated' class ($3 \cdot 8 \pm 0 \cdot 53$ cm.), and is lower in pregnant, lactating, and 'resting' females (respectively $2 \cdot 78 \pm 0 \cdot 15$ cm., $1 \cdot 93 \pm 0 \cdot 34$ cm. and $1 \cdot 93 \pm 0 \cdot 29$ cm.). The existence of a cycle of follicular activity has been demonstrated in pregnant females, reaching a peak in mid-pregnancy (November/December). At this time the follicles enlarge, but do not mature, owing to the presence of the active corpus luteum. No accessory corpora lutea form during pregnancy as happens in some other mammals. From the follicle sizes it appears that there are periods of follicular activity in early lactation and at the end of lactation.

6. Ovulation probably occurs when the follicle attains a diameter of about 7 cm., collapsing to about 4 cm. immediately after ovulation and then, as the corpus luteum forms, increasing to $8 \cdot 28 \pm 0 \cdot 82$ cm. in the corpus luteum of the cycle, or to $11 \cdot 44 \pm 0 \cdot 15$ cm. if pregnancy supervenes. There is no reason to suppose that pseudopregnancy occurs. It is possible that there is a slight tendency for the right ovary to ovulate more frequently than the left in baleen whales, but the data for blue and fin whales do not show a significant difference. There is a marked tendency for ovulation to occur in the vicinity of the anterior pole of the ovary. The mean weight of the corpus luteum of ovulation is $0 \cdot 375$ kg. (range $3 \cdot 4$ g.–$1 \cdot 5$ kg.) and the mean weight of the corpus luteum of pregnancy is $0 \cdot 881$ kg. (range $0 \cdot 2$–$2 \cdot 4$ kg.). Various morphological types of corpora lutea are described and related to the modes of formation; vesicular corpora lutea constitute $17 \cdot 1 \%$ of all corpora lutea. Accessory corpora lutea comprised only $3 \cdot 7 \%$ of all corpora lutea examined; they have a mean diameter of $3 \cdot 88 \pm 0 \cdot 80$ cm. and a weight of about 45 g. The size ranges of corpora lutea of ovulation and pregnancy are large, so that these bodies cannot be distinguished from one another on the basis of size, and no certain diagnostic features have been found.

7. There is no significant difference in the mean size of corpora albicantia in the ovaries of pregnant, lactating, and 'resting' females; they have a mean diameter of $2 \cdot 5$ cm. and a mean weight of about 10 g. The various morphological types of corpora lutea are reflected by the corpora albicantia and, in particular, the incidence of vesicular or radiate corpora albicantia is not significantly different from the proportion of vesicular corpora lutea.

It appears that corpora lutea regress to a constant proportion of their initial size, and as this is large they remain visible throughout life.

Three age groups of corpora albicantia have been identified on the basis of anatomical and histological changes associated with regression. 'Young' corpora albicantia have a mean diameter of $4 \cdot 01$ cm. and a weight of 41 g.; the values for 'medium' corpora albicantia are $2 \cdot 94$ cm. and 15 g., and for 'old' corpora albicantia $2 \cdot 01$ cm. and 5 g.

The ratio of 'young' to 'medium' corpora albicantia in the ovaries is 1 : 2 and it is shown that the 'young' corpora albicantia probably represent one year's increment of corpora and take about three years to regress to 'old' corpora albicantia. From this it can be calculated that the mean annual increment of corpora is probably about $1 \cdot 4$–$1 \cdot 5$ (although there is a possibility that the rate is only half this value), and as the corpora persist throughout life, counts of them may be used to determine age.

8. Two other structures in the ovaries are described, the corpora aberrantia and the corpora atretica. The former are included in the corpora counts (as corpora albicantia) for the purpose of age-determination, but the latter are ignored.

9. It has been possible to confirm earlier work on the correlation between the attainment of physical maturity and the accumulation of 14–15 corpora lutea and corpora albicantia. The frequency distribution of the number of corpora shortly after puberty (baleen group v), and at the threshold of physical

maturity, have been compared. These frequency curves are found to be very similar in shape and range, with standard deviations of respectively 3·3 and 3·94 corpora. This amount of variation is almost entirely explained by the spread in the ages at puberty, and suggests that there is a very regular annual increment of corpora, which is difficult to explain on the basis of a polyoestrous sexual cycle.

10. Histological examination of a series of fin whale testes indicates that the period of maximum activity extends from about April to July and is minimal in January and February. The seminiferous tubules undergo a seasonal variation in diameter, decreasing progressively from 164 μ in October to 140 μ in February and rising again to 165 μ in April. The maximum diameter recorded (241 μ) was from March. Reference to the incidence of diatom film (which is absent in lower latitudes), indicates that on entering antarctic waters the tubule diameter is about 170 μ, falling to 140 μ when the diatom film is well developed. In immature males the tubule diameter averaged 79 μ and in one near to puberty 102 μ.

11. A mean curve of foetal growth is given and from this the conception dates of individual foetuses can be estimated. 12 June is estimated to be the mean date of pairing, but the frequency-distribution of conceptions is skewed, with a peak in May/June. It is estimated that 77 % of foetuses are conceived between April and August, and only about 6 % between October and March. As the gestation period is about 11¼ months the frequency distribution of births can easily be obtained. Annual variations in the timing of the breeding season are discussed.

12. Earlier estimates of the mean length of the female at puberty (65·25 ft.) have been confirmed on the larger samples now available; the standard deviation of the length at puberty is 2·07 ft., but this is influenced by the post-mortem history of individuals and the variance in life is probably much less. The average age at puberty based on ear-plug ages and ovarian examination is estimated to be about 5 years, ranging from 3 to 8 years in the relatively small sample available.

13. The state of the mammary gland is used to diagnose nulliparous and primiparous females. Of 88 females pregnant for the first time 68 % had only one corpus luteum and only 9 % had more than two corpora. The mean number of ovulations preceding conception was 1·42.

The pairing season of primiparous females was estimated, like that for all females, from foetal length data, and it is found that the median date of pairing is about 21 July. That is about 4–6 weeks later than multiparous females, and the frequency curve of conceptions is symmetrical, not skewed.

The rate of growth in length for females in their first pregnancy can be determined, employing foetal age as a time-scale. The average female grows from 65·25 ft. to about 68–69 ft. during the twelve months following puberty. There appears to be a marked increase in the growth-rate related to the short annual period of intensive feeding. The growth in the following year has also been studied.

14. Evidence is presented which suggests that ovulation is spontaneous. It appears that at puberty there is a single ovulation, and if the female is not successfully mated she goes into anoestrus without experiencing further ovulatory cycles at this time. Although puberty is normally attained in July, it may also be attained outside the normal pairing season, mainly in November, December, and January. Then also there is a monoestrous cycle, but it is almost invariably unsuccessful because, it is believed, the males are sexually inactive at this time.

The relation of puberty to the migratory cycle is discussed. In the majority of females puberty is preceded by a period of intensive feeding in the Antarctic, when growth is probably rapid, but the main exteroceptive factor bringing about the first ovulation appears to be the period of increasing day lengths associated with the northward migration. There is a second, subsidiary period when other females attain puberty in December, after a southward migration, during which they also experience increasing day lengths. It is suggested that puberty is initiated by a combination of age and increasing day lengths, the light threshold becoming lower with increasing age.

15. The pairing season of multiparous females is investigated as before from foetal length data. The peak conception period is from April to July, with 8 June as the median date of pairing, and the curve is skewed, with a long tail from July to December. Less than 13% of all multiparous conceptions are estimated to take place before May. The average age of females pairing in March and April is much higher than for later months but, apart from this older group and the primiparous group, age does not influence the conception date.

16. Data on the incidence of females which are concurrently lactating and pregnant are given, and suggest that some 18% of females conceive at a post-partum ovulation. Evidence is presented which suggests that nearly all multiparous females experience a post-partum heat, and that a proportion of primiparous females do not. This is inferred from the relative sizes of the corpora albicantia in different classes of mature females, and from the presence in the ovaries of lactating females of anomalous corpora which resemble corpora aberrantia in their histology.

Loss of a near-term foetus, a stillbirth, or loss of a young calf, is probably followed by an oestrous cycle comparable with normal post-partum heat. The termination of pregnancy at an earlier stage is probably followed by ovulation at the ovulatory period which would normally occur next.

17. A small proportion of females in late lactation are found to have recently ovulated, and some 14% of 'resting' females are also found to have ovulated recently and to have a corpus luteum of ovulation in the ovaries. The incidence of diatom film is low in both lactating and recently-ovulated females, suggesting that they are females which have only recently entered antarctic waters, and that they have therefore ovulated either during or just after the southward migration.

The incidence of recent ovulations in antarctic waters is not constant throughout the summer months, but falls progressively from October/November to April. Evidence is presented which strongly suggests that almost all fin whale females experience a post-lactation ovulation, and a theoretical curve based on this hypothesis, which indicates the entry of post-lactation females into the antarctic summer population, is in close agreement with one showing the monthly antarctic catch. It is concluded that 50% of non-pregnant mature females are south of the Antarctic Convergence by mid-December, and that December is the average time of the post-lactation ovulation. This is in agreement with the time of the suppressed oestrous cycle of pregnant females, and suggests that identical exteroceptive factors are responsible for the regulation of this cycle in these two classes of females. Very few pregnancies are initiated at this time, mainly owing to the absence of sexually active males.

18. The cyclical activity of the mammary glands is briefly described. The criterion of lactation which is adopted is the presence of apparently normal milk in the glands, but this is not completely valid because it has been shown that probably about 25% of such females in antarctic waters have recently ceased to secrete milk and are weaning, or have just weaned, the calf. The average month of weaning is estimated to be December, and the lactation period is about 7 months. The incidence of diatom film, and the ages of foetuses in females simultaneously lactating and pregnant, suggest that these females do not usually enter antarctic waters until they are just about to wean the calf.

The relative abundance of lactating females in antarctic waters in different months is examined, and it is concluded that they are not present in representative numbers in the early part of the whaling season. It is suggested that the southward migration of females with suckling calves is dependent on, and limited by, seasonal changes in sea temperature, and that the critical surface temperature is about 0° C. Thus, the influx of lactating females is earlier at South Georgia than on the pelagic whaling grounds further south; probably over 50% of females wean their calves before entering South Georgia waters, and over 80% do so before they enter the pelagic whaling grounds.

19. The relation of the sexual cycle to the migratory cycle is discussed. It is suggested that, as in females at puberty, the biannual ovulatory periods are primarily related to the twice-yearly period of

increasing day lengths associated with the north and south migrations. Animals remaining in one latitude or undertaking small migrations are only subjected to one period of increasing and one of decreasing day lengths annually.

This hypothesis agrees both generally and in detail with the type of female sexual cycle outlined above, but for males it is necessary to assume that a refractory period follows the extended winter period of sperm production, as in some male birds, and that the spring migration does not initiate a second period of rut.

The evidence strongly suggests that the female fin whale is not polyoestrous, as earlier workers have assumed, but seasonally monoestrous.

20. An explanation of the assumed biannual formation of ear-plug laminations is advanced. It seems likely that the biannual hormonal cycle, regulated by changes in day lengths associated with the long migrations, may be responsible. Thus during each migration there is a rise in the amounts of circulating oestrogens, associated with oestrus, and it is suggested that this is responsible for the formation of a keratinous layer in the epithelium contributing to the growth of the ear-plug.

21. The possibility of variation in fertility with age is examined. It is shown that with increasing age there is probably a slight increase in the occurrence of multiple ovulations. Details are given of one case in which 13 corpora lutea were formed as a result of a multiple ovulation, but this is exceptional. In 22 out of 27 cases of multiple ovulation only two corpora lutea were formed.

The proportion of sexually active females in different age groups has also been examined, and it is shown that age changes in fertility are slight; the youngest females show slightly lower fertility, which is probably maximal at ages of about 15–25 years, and may decline at ages in excess of about 30–40 years.

Evidence is presented which suggests that up to a point fertility is directly proportional to the intensity of whaling, and has increased to a maximum level above which it appears that no further increase is possible in this species. The conclusions reached in this paper about the incidence of, for example, post-partum conceptions, probably apply to fin whale populations in which fertility is maximal. With post-partum conceptions assumed to be 18%, the average conception rate per female is 0·59 per year.

22. The annual rate of ovulation can be calculated from the type of sexual cycle which has now been established. These calculations suggest an annual rate of ovulation of 1·43, which is very close to the higher estimate obtained from a consideration of the regression of corpora albicantia. Allowing for possible causes of error it is concluded that the average annual increment of corpora is 1·43±0·1.

No firm evidence about the rate of accumulation can be obtained from the recovery of whale marks together with ovaries for 10 female fin whales, owing to the small size of this sample and the uncertainty about the age at marking.

23. For estimating individual ages of females taken in the Antarctic the number of corpora is divided by 1·43 and to the result is added $4\frac{1}{2}$ years to allow for the immature period. Allowing for the variation in the age at puberty, the accuracy of the method is such that about 90% of females should be within ±3 years of the estimate.

Ages determined in this way are in close agreement with the results obtained by other methods, namely baleen plates and ear-plugs. When individual ear-plug ages are plotted against the corresponding ovarian ages, it is found that 72% of the latter lie within ±3 years of the regression line showing an exact correlation, and are symmetrically distributed; 82% lie within ±4 years.

In drawing up survival curves or growth curves based on large samples the variation in individual ages becomes unimportant.

24. Survival curves are given for area II females which, when plotted logarithmically, approximate to the diagonal type, and this implies a more or less constant mortality with respect to age. It appears

that total immature mortality up to 5 years amounted to about 53% if the population which the sample represents can be assumed to be stable.

The relation between the catches and the age structure of the population is briefly discussed, and it is shown that for the segment of the dynamic curve between 9 and 26 years, corresponding to a period when fishing mortality was relatively small, the annual adult mortality rate was probably about 9·2%. The oldest animals in this sample are estimated to have been 42½ years old, and it is suggested that the specific longevity of the female fin whale is likely to be about 50 years.

25. Length-at-age data for area II females above 5 years of age are presented, the ages estimated from corpora counts. The von Bertalanffy growth equation has been fitted to this data. This gives a theoretical curve for which $l_t = 73 \cdot 0 \, (1 - e^{-0 \cdot 45(t - 0 \cdot 368)})$, and corresponds very closely to the observed mean values. This curve has been extrapolated back to 3 years, and is completed by including observed values for foetal growth and the estimated length at age corresponding to weaning. It provides additional evidence of the validity of ovarian corpora counts for age-determination.

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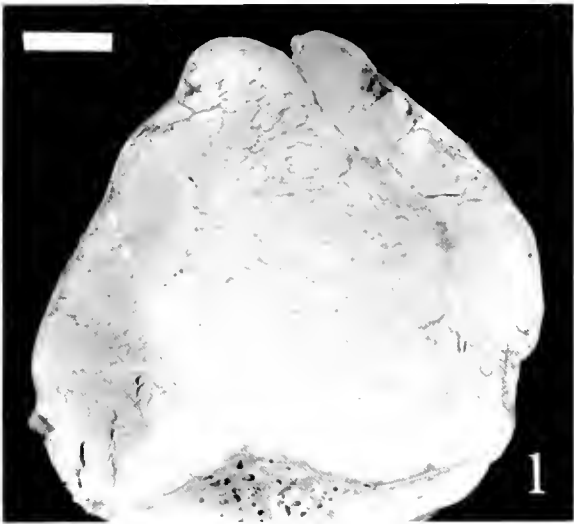* These papers also appear in Collected Reprints of the National Institute of Oceanography.

PLATE IV

Fig. 1. Section of a typical corpus luteum of pregnancy (bar = 1 cm.).

Fig. 2. Photomicrograph of a thick cleared section of a corpus luteum
to show vascular and avascular septa (bar = 1 mm.).

Fig. 3. Photomicrograph of corpus luteum of a pregnant female; foetus
0.47 m; fixed Zenker-formol, post-osmicated, not counterstained
(bar = 200 μ).

Fig. 4. Photomicrograph of corpus luteum of a pregnant female; foetus
2.47 m; treatment as in fig. 3 (bar = 200 μ).

Fig. 5. Photomicrograph of corpus luteum of a pregnant female; foetus
5.15 m; treatment as in fig. 3 (bar = 500 μ).

Fig. 6. Photomicrograph of ovarian cortex of immature female, body
length 54 feet, showing primary follicles; fixed Bouin, stained
Masson's Trichrome (bar = 200 μ).

PLATE IV

Fig. 1. Section of a typical corpus luteum of pregnancy (bar = 1 cm.).

Fig. 2. Photomicrograph of a thick cleared section of a corpus luteum to show vascular and avascular septa (bar = 1 mm.).

Fig. 3. Photomicrograph of corpus luteum of a pregnant female; foetus 0·47 m; fixed Zenker-formol, post-osmicated, not counterstained (bar = 200 μ).

Fig. 4. Photomicrograph of corpus luteum of a pregnant female, foetus 2·47 m; treatment as in fig. 3 (bar = 200 μ).

Fig. 5. Photomicrograph of corpus luteum of a pregnant female; foetus 5·15 m; treatment as in fig. 3 (bar = 500 μ).

Fig. 6. Photomicrograph of ovarian cortex of immature female, body length 54 feet, showing primary follicles; fixed Bouin, stained Masson's Trichrome (bar = 200 μ).

PLATE IV

PLATE V

Fig. 1. Section of a typical 'young' corpus albicans (bar = 1 cm.).

Fig. 2. Photomicrograph of 'young' corpus albicans, fixed Zenker-formol, post-osmicated, not counterstained (bar = 1 mm.).

Fig. 3. Photomicrograph of 'medium' corpus albicans, treatment as fig. 2 (bar = 1 mm.).

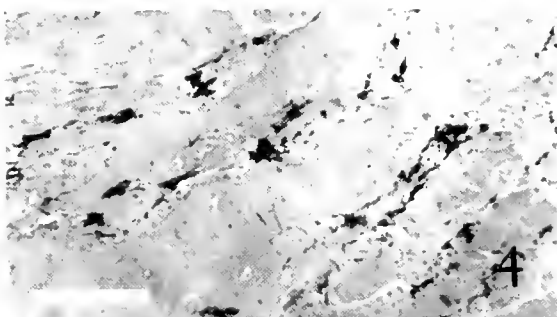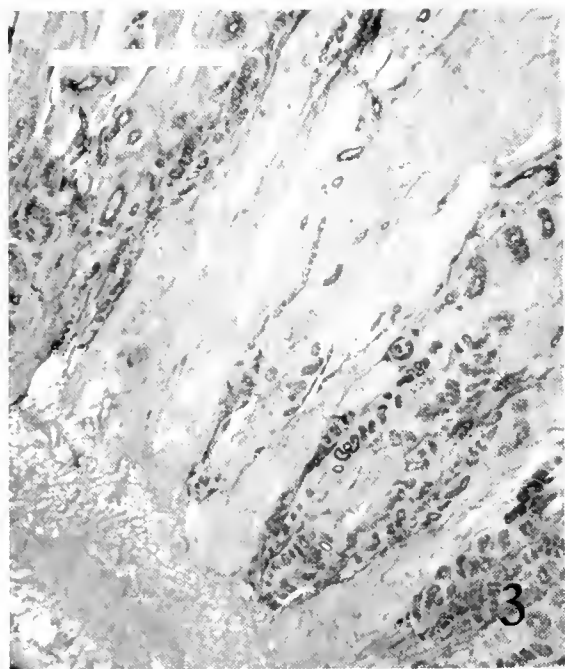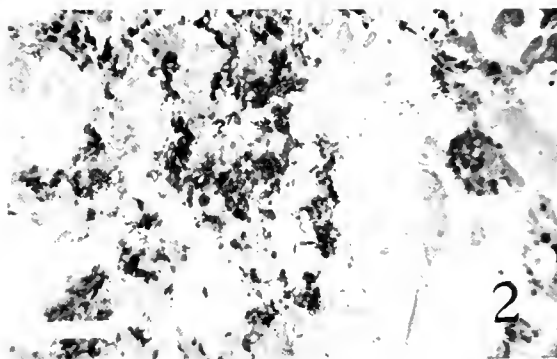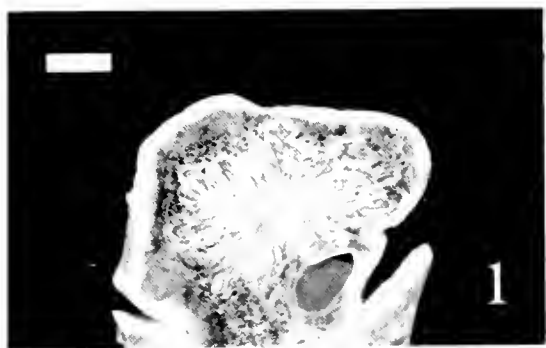Fig. 4. Photomicrograph of 'medium' corpus albicans, fixed Bouin, stained Masson's Trichrome (bar = 1 mm.).

Fig. 5. Photomicrograph of anomalous corpus albicans from lactating female (Text-fig. 46 c), treatment as fig. 2 (bar = 200μ).

Fig. 6. Photomicrograph of corpus albicans shown in fig. 3 to show arrangement of lipoids (bar = 200μ).
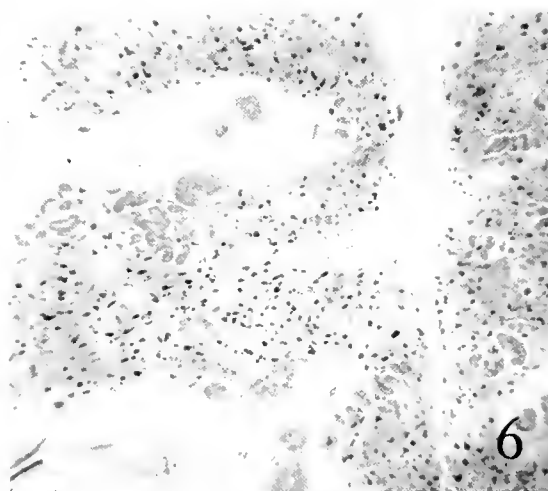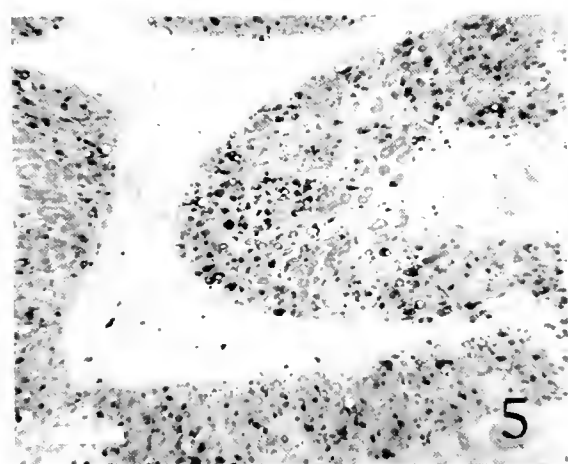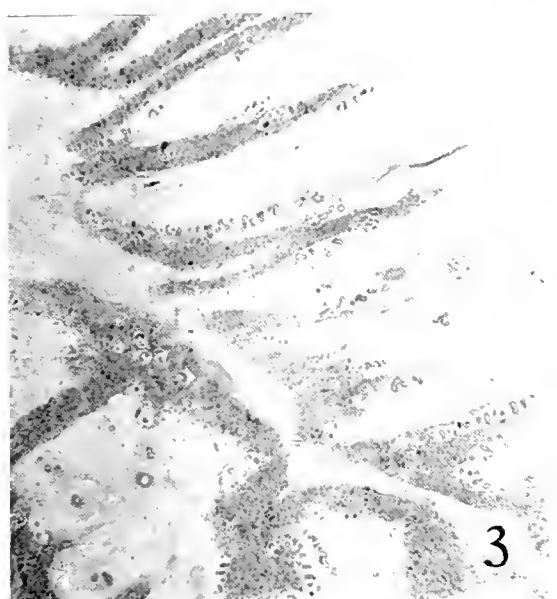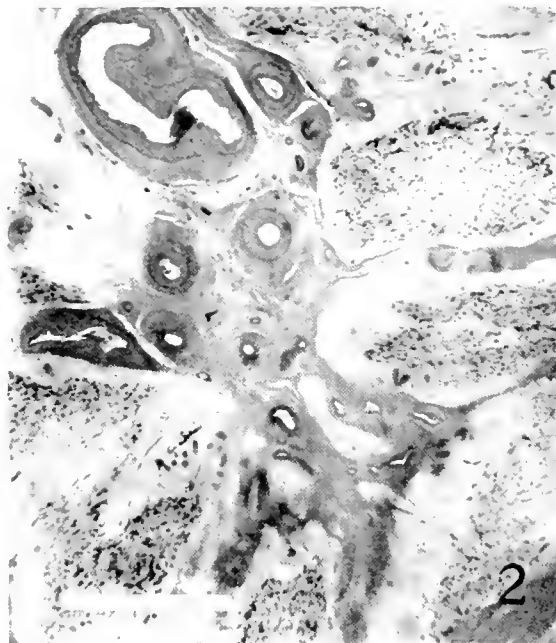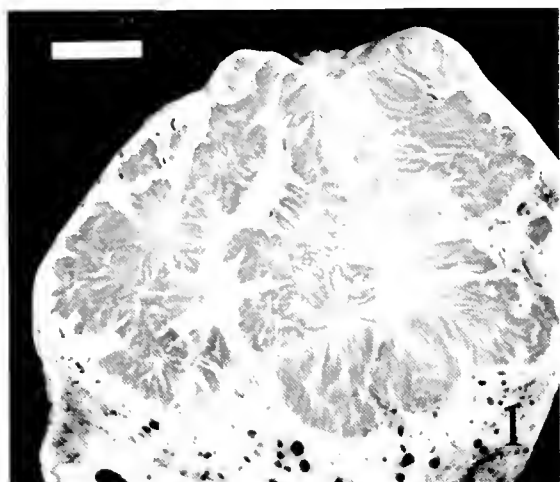
PLATE V

PLATE VI

Fig. 1. Section of typical 'old' corpus albicans (bar = 1 cm.).

Fig. 2. Photomicrograph of old corpus albicans; fixed Zenker-formol, post-osmicated, not counterstained (bar = 200μ).

Fig. 3. Photomicrograph of typical radiate corpus albicans; fixed Bouin, stained Haematoxylin and eosin (bar = 1 mm.).

Fig. 4. Photomicrograph of old corpus albicans, treatment as fig. 2 (bar = 1 mm.).

Fig. 5. Photomicrograph of old corpus albicans; treatment as fig. 2 (bar = 1 mm.).

Fig. 6. Photomicrograph of old corpus albicans; treatment as fig. 2 (bar = 1 mm.).

Fig. 7. Photomicrograph of old corpus albicans; treatment as fig. 2 (bar = 1 mm.).
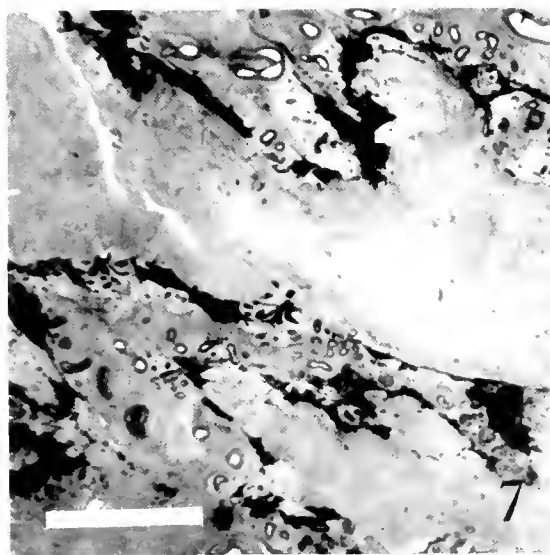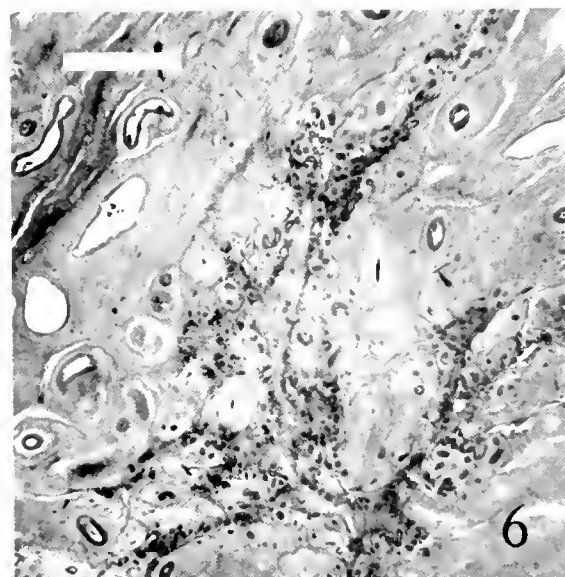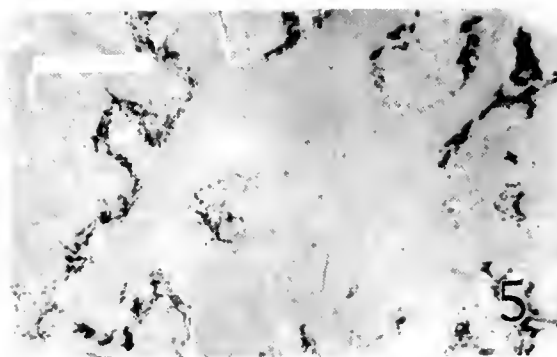
PLATE VII

Fig. 1. Photomicrograph of old corpus albicans; fixed Bouin, stained Haematoxylin and eosin (bar = 0·5 mm.).

Fig. 2. Photomicrograph of old corpus albicans, fixed Bouin, stained Van Gieson (bar = 1 mm.).

Fig. 3. Photomicrograph of corpus aberrans (Text-fig. 23a); fixed Zenker-formol, post osmicated, not counterstained (bar = 0·5 mm.).

Fig. 4. Photomicrograph of corpus aberrans (Text-fig. 23c); fixed Bouin, stained Masson's Trichrome (bar = 200μ).

Fig. 5. Photomicrograph of corpus atreticum (Text-fig. 23d); treatment as fig. 3 (bar = 1 mm.).

Fig. 6. Photomicrograph of corpus aberrans shown in fig. 4, but treatment as fig. 3 (bar = 200μ).

Fig. 7. Photomicrograph of part of corpus atreticum shown in fig. 5 (bar = 200μ).